

## Anatomical Structure of Fruits and Evolution of the Tribe Sorbeae in the Subfamily Maloideae (Rosaceae)

Hiroyuki IKETANI<sup>1)</sup> and Hiroyoshi OHASHI

Biological Institute, Faculty of Science, Tohoku University,  
Sendai, 980, JAPAN

バラ科ナシ亞科ナナカマド連における果実の解剖学的構造と進化

池谷祐幸<sup>1)</sup>, 大橋広好

東北大学理学部生物学教室 980 仙台市青葉区荒巻字青葉

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Structures of fruits of 61 species of 17 genera of the tribe Sorbeae (Rosaceae-Maloideae) are anatomically examined. Structure of the pulp is different at the generic level in Sorbeae. Nearly half of the genera examined have a homogeneous pulp structure consisting of parenchyma and few or no stone cells. In contrast, the other genera have several kinds of heterogeneous pulp structure consisting of parenchyma, stone cells, and pigment cells. The inner epidermis does not become sclerified in most of genera, but in some genera it becomes sclerenchymatous.

Hypothetical evolutionary trends of the structure of the fruits in Maloideae are proposed. The fruit of Crataegeae is inferred as more primitive than that of Sorbeae. Pulp structure of Sorbeae may have been evolved through loss of sclerenchymatous cells and/or through specialized distributional pattern of sclerenchymatous cells and pigment cells, e. g., clusters of stone cells in the center of the flesh (*Pourthiaeae*), clusters of large sized pigment cells and/or stone cells in the whole part of the flesh (*Micromeles* and subgenera *Aria* and *Chamaemespilus* of *Sorbus*), and clusters of stone cells in the inner flesh (subgenus *Torminalia* of *Sorbus*). Phylogenetic relationships of the genera of Sorbeae are inferred based on these evolutionary trends.

### Introduction

The subfamily Maloideae is divided into two tribes, Crataegeae and Sorbeae, based on characters of the fruit (Koehne 1890, Schluze-Menz 1964, Kovanda 1965, Phipps et al. 1990). In Crataegeae almost all parts of the carpel become bony in the mature fruit and the fruit becomes drupe-like. This does not occur in the fruits of the tribe Sorbeae.

Decaisne (1874) first recognized the diversity of pulp structure in Sorbeae. He discovered the heterogeneous nature of the pulp with normal-sized parenchyma and large cells in *Pourthiaeae*, *Micromeles*, and subgenus *Aria* (including *Chamaemespilus*) of *Sorbus*. This was not evaluated as a taxonomic character until the middle of this century. Gabrielian (1958) and Kovanda (1961) re-examined anatomical characters of fruits

of European species of *Sorbus* and concluded that pulp structure is very useful for distinguishing the subgenera of *Sorbus*. However, since they did not investigate *Pourthiaeae*, *Micromeles*, and the Asiatic species of *Sorbus*, it was not clear whether the pulp structure is truly distinctive among the subgenera of *Sorbus* or not, and whether the heterogeneous nature of the pulp of these three taxa is homologous or not.

It is well known that the degree of density of stone cells in the pulp is a useful character for distinguishing some genera of Sorbeae. For example, there are many stone cells in the pulp of *Pyrus*, but only a few or no stone cells in that of *Malus*, with the exception of sections *Docyniopsis* and *Eriolobus* (Rehder 1940). Structures of the innermost part of the fruit flesh have also been recognized as different among genera. It has been described as cartilaginous, membranous, or leathery (e.g., Hutchinson 1964, Robertson et al. 1991). However, except for some species with edible fruits, these characters have not been well investigated.

As mentioned above, anatomical characters of the fruit of Sorbeae have been recognized as useful taxonomic characters for distinguishing genera since the last century, but they have not been well investigated. Almost all anatomical studies of the fruit have been performed in *Malus domestica* Borkh. (e.g., MacArthur and Wetmore 1939, MacDaniels 1940, Tukey and Young 1942, Roth 1977) and *Pyrus communis* L. (e.g., MacDaniels 1940, Sterling 1954, Roth 1977). Except for Gabrielian's (1958) and Kovanda's (1961) works in *Sorbus*, no anatomical works on the fruits of Sorbeae have been performed from a systematic point of view.

In this study, we report the anatomical characters of the fruit of the genera of Sorbeae, with special attention to the structure of the pulp,

distribution of stone cells, and structure of the inner epidermis and neighboring cells of the fruit. Based on these data we will attempt a systematic evaluation of these characters in this tribe.

### Materials and methods

Seventy-three species belonging to 24 genera of the Maloideae, of which 61 species of 17 genera in the tribe Sorbeae and 12 species of 7 genera in the tribe Crataegeae, were studied. Fruits examined were either fresh or dried, or from herbarium specimens. Sources of materials and voucher specimens are listed in the appendix.

Fresh fruits were fixed in FAA (Five parts stock formalin; five parts glacial acetic acid; 90 parts 70% ethanol). Dried fruits were softened with a solution containing equal volumes of glycerol and 10% aerosol-OT for about a week at room temperature. After these treatments all materials from fresh or dried fruits were softened with 15% hydrofluoric acid for about two weeks at room temperature. Then they were washed with running water and dehydrated through an n-butanol series and embedded in paraplast (melting point 57–58°C) for microtoming. Some exceptionally hard or large specimens were dehydrated with an ethanol-ethyl ether series and embedded in celloidin, or double embedded in celloidin-paraplast (Johansen 1940). Paraplast sections and double embedded sections cut 15–20 µm in thickness were either triple stained with Heidenhain's Hematoxylin, Safranin O and Fastgreen FCF, or double stained with Safranin O and Fastgreen FCF. Celloidin sections cut 50–100 µm in thickness were stained with Safranin O and Fastgreen FCF. All stained sections were mounted in Entellan New (Merck Co. Ltd.).

Prepared specimens were observed with a normal optical microscope. Specimens were also observed in crossed polarized light for the presence

of sclerenchymatous cells.

### Results

**Terminology** The so-called fruit of the subfamily Maloideae is a false fruit called a pome that consists of carpels and a fleshy enlarged hypanthium (sometimes called calyx tube) surrounding or fused to them (Fig. 1). Bony parts in the mature fruit of the tribe Crataegeae are sometimes recognized as the endocarp, and the fruit is called a drupe or pyrene (Lindley 1821, Kovanda 1965, Kalkman 1973). Actually, however, not only the innermost part of the carpel (true endocarp) but also almost the other part of carpel becomes bony as described by Sterling (1964), and the hypanthium becomes fleshy (Figs. 2–6). So, this kind of fruit is not the same as that of true drupe, as in *Prunus*. In the tribe Sorbeae generally both parts of the fruit derived from the carpel and the hypanthium become completely fleshy and cannot be separated histologically. Fahn (1990) recognized the border between the dorsal bundles of the carpel and the innermost prominent bundles of the hypanthium. We follow him and we called the outer part of this border "outer flesh" and the inner part "inner flesh" as used by Olson and Steeves (1982).

In true fruits, exocarp, mesocarp, and endocarp are often distinguished in the pericarp. In many fruits of Sorbeae, it is impossible to distinguish mesocarp and exocarp, because these two parts become fleshy as outer flesh. Moreover, these three terms are sometimes confused in the fruits of Maloideae, and, in some cases, mesocarp is used as the whole fleshy part of the pome (Camefort and Boué 1980). So, in this study, we don't use these three terms.

**Description of the structure of the fruit** Degree of density of sclereids and pigment cells in the flesh differs in genera of Sorbeae. Also, distributional

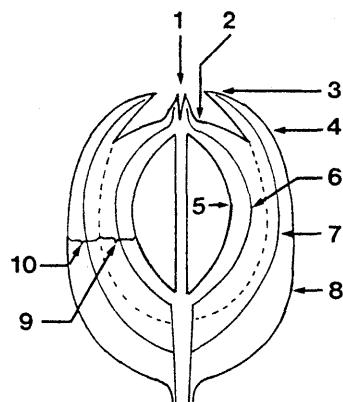


Fig. 1. Explanatory scheme of the general structure of the fruit of Sorbeae. 1: style. 2: apical part of the inner flesh. 3: sepal. 4: a portion of free hypanthium. 5: inner epidermis. 6: dorsal bundle of the carpel. 7: innermost prominent bundle of the hypanthium. 8: epidermis. 9: inner flesh. 10: outer flesh. Broken line indicates the border between the part derived from the carpel (inner flesh) and that derived from the hypanthium (outer flesh).

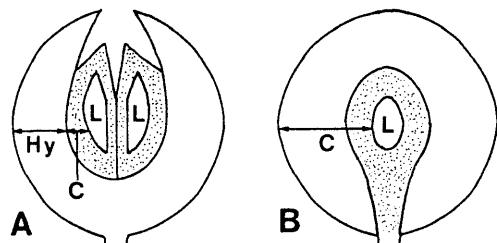
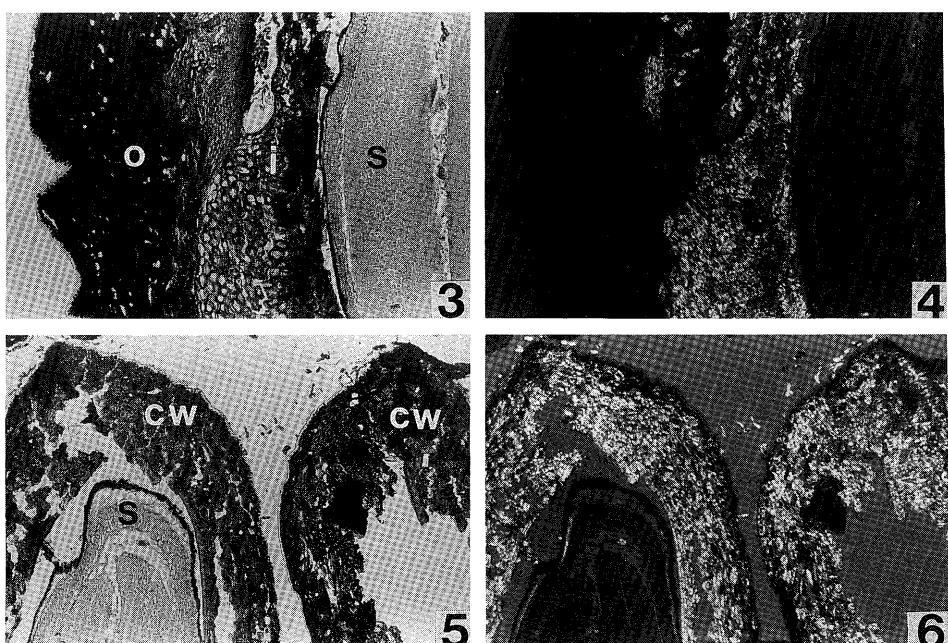


Fig. 2. Schematic drawing of the fruit structure of Crataegeae and *Prunus*. A: Crataegeae, B: *Prunus*. Hy: part derived from the hypanthium. C: part derived from the carpel. L: locule. The dotted part represents sclerenchymatous tissue.

pattern varies in the genera. The shape of sclereids are isodiametric (= stone cells) in the most part of flesh, but in the inner epidermis and neighboring cells it is sometimes radially elongated. In many cases the apical part of the inner flesh and the inner epidermis and neighboring cells have some different pulp structure from the other part of fruit. Therefore, we describe these parts separately. Hence, a fruit is divided into the following six parts; inner epidermis and neighboring cells, inner flesh (except for the apical part of the inner flesh),



Figs. 3–6. Fruit of *Hesperomeles heterophylla* (Gillis et Powman 10234). Figs. 3, 4: Longitudinal section. All parts of the inner flesh (the part derived from the carpel) become sclerenchymatous, but the outer flesh (the part derived from the hypanthium) does not.  $\times 29$ . Figs. 5, 6: Longitudinal section through apical part of the carpel. Nearly all parts of the carpillary wall except for the epidermis and neighboring cells become sclerenchymatous.  $\times 29$ . Figs. 4 and 6: same field as Figs. 3 and 5, respectively, seen in crossed polarized light. o: outer flesh, i: inner flesh, cw: carpillary wall, s: seed.

outer flesh, hypodermis, apical part of the inner flesh, and a portion of free hypanthium and sepals (Fig. 1). Results are summarized in Table 1.

#### *Sorbus* subgenus *Sorbus* (Figs. 9, 10)

Inner epidermis is not generally sclerified. Stone cells appear sparsely or rather densely in the inner flesh and outer flesh, and usually appear rather densely in the apical part of the inner flesh. Pigment cells are generally absent or rare except for

the hypodermis. A portion of free hypanthium and sepals become fleshy except for the tip of sepals.

#### *Sorbus* subgenus *Torminalia* (Figs. 11–13)

Inner epidermis and the neighboring cells are not generally sclerified. Large clusters of stone cells appear densely in the inner flesh and in the apical part of the inner flesh. The size of each stone cell is not clearly larger than that of parenchymatous cell. Pigment cells are few in the inner flesh but

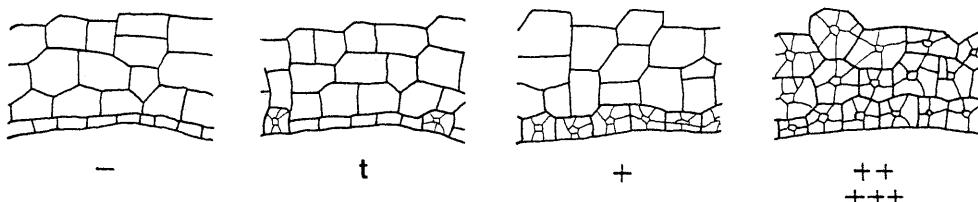


Fig. 7. Schematic drawings of the anatomical structure of inner epidermis and neighboring cells, classified into five types. -: Inner epidermis does not become sclerenchymatous. t: Inner epidermis becomes partly sclerenchymatous. +: Inner epidermis becomes wholly sclerenchymatous. ++: Inner epidermis and neighboring cells become sclerenchymatous. +++: In addition to ++, inner flesh also becomes completely sclerenchymatous.

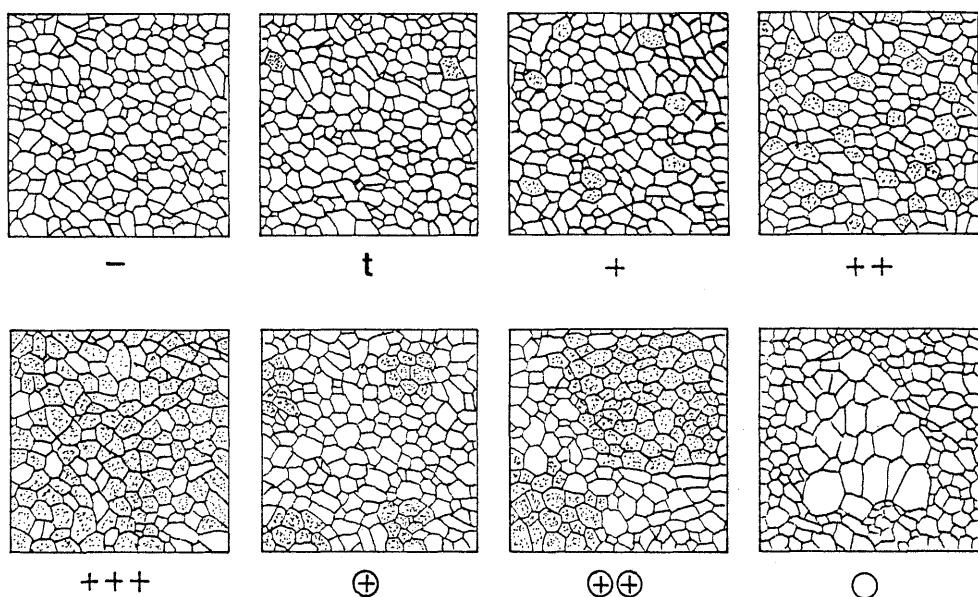


Fig. 8. Schematic drawings of the fleshy part of the fruit, classified into eight types. -: Stone cells (or pigment cells) absent. t: Stone cells (or pigment cells) rare. +: Stone cells (or pigment cells) scattered. ++: Stone cells (or pigment cells) dense. +++: Tissue almost exclusively composed of stone cells (or pigment cells). ⊕: Clusters of stone cells (or pigment cells) present. ⊕⊕: Large clusters of stone cells (or pigment cells) present. O: Large clusters of large sized parenchymatous cells present.

appear densely in the outer flesh. A portion of free hypanthium partly becomes fleshy but sepals become shriveled up (Fig. 13).

*Sorbus* subgenus Chamaemespilus (Fig. 14) and subgenus Aria (Figs. 15–20)

Inner epidermis is not generally sclerified. Clusters of heterogeneous cells appear in the inner flesh and outer flesh. In *Sorbus chamaemespilus*, *S. hayastana* and *S. kusnetzovii*, these clusters consist of parenchymatous cells or parenchymatous pigment cells (Figs. 14–16) or only a few stone cells appear in these clusters of the inner flesh besides pigment cells and parenchyma. In the Asiatic species of Aria (*S. cuspidata*, *S. lanata* and *S. xanthoneura*), clusters of the inner flesh consist mainly of stone cells and those of the outer flesh consist mainly of pigment cells (*S. xanthoneura*; Figs. 17, 18) or sclerenchymatous pigment cells (*S. cuspidata* and *S. lanata*; Figs. 19, 20). The apical part of the inner flesh has

a few or rather many stone cells. A portion of free hypanthium and sepals become fleshy except for the tip of sepals, but in Himalayan species (*S. cuspidata* and *S. lanata*), which have almost completely inferior ovary, sepals are persistent but become scarcely fleshy.

#### *Micromeles* (Figs. 21–24)

Inner epidermis is not generally sclerified. Clusters of stone cells appear in the inner flesh similar to those of subgenera Aria and Chamaemespilus of *Sorbus*. In the inner flesh these clusters are usually composed of stone cells which usually have vacuoles rich in pigments and in the outer flesh they are mainly composed of sclerenchymatous pigment cells. A portion of free hypanthium and sepals fall off after anthesis.

#### *Aronia* (Figs. 25, 26)

Inner epidermis is not sclerified. Stone cells are sparsely or rather densely distributed in the inner and outer flesh and rather densely distributed in

Table 1. Anatomical characters of the fruit of taxa examined\*.

Species	I E	I F	O F	H D	A I F	F H
<i>Sorbus</i> subg. <i>Sorbus</i>						
<i>S. commixta</i> Hedl.	~t	+	+	-	++	+
	-	-	-	+	-	-
<i>S. esserteauiana</i> Koehne	t ~+	++	++	+	++	++
	-	-	-	++	-	+
<i>S. gracilis</i> C. Koch	-	+	-	-	++	++
	-	-	-	++	-	-
<i>S. matsumurana</i> Koehne	-	-	-	-	-	-
	-	-	-	+	-	-
<i>S. pohuashanensis</i> Hedl.	t ~+	+	+	-	++	+
	-	-	-	++	+	+
<i>S. sambucifolia</i> Roem.	-	++	++	-	++	+
	-	+	t	+	-	-
<i>S. scalaris</i> Koehne	t ~+	++	++	-	++	+
	-	-	-	++	+	+
<i>Sorbus</i> subg. <i>Torminalia</i>						
<i>S. torminalis</i> Cr.	-	⊕⊕	+	-	++	not
	t	+	+++	+++	+	fleshy
<i>Sorbus</i> subg. <i>Chamaemespilus</i>						
<i>S. chamaemespilus</i> Cr.	-	(⊕) -	-	-	N D	N D
	-	⊕	⊕	++	++	++
<i>Sorbus</i> subg. <i>Aria</i>						
<i>S. cuspidata</i> Hedl.	-	⊕	-	-	⊕⊕	-
	-	-	⊕	++		⊕
<i>S. hayastana</i> Gabr.	-	⊕ ○	○	-	++	○
	-	-	-	-	-	-
<i>S. kusnetzovii</i> Zinserl.	-	(⊕) ○	○	-	-	○
	-	-	-	-	-	-
<i>S. lanata</i> C. Koch	~t	⊕	-	+	++	⊕
	-	-	⊕	++	-	
<i>S. xanthoneura</i> Rehder	-	⊕⊕	-	-	++	++
	-	-	⊕⊕	++	+	+
<i>Micromeles</i>						
<i>M. alnifolia</i> C. Koch	-	⊕⊕	-	-	++	
	-	-	⊕⊕	⊕	+	deciduous
<i>M. caloneura</i> Stapf	t	⊕	-	-	N D	
	-	⊕	⊕⊕	++	N D	deciduous
<i>M. corymbifera</i> Kalkman	N D	⊕⊕	-	+	N D	
	N D	-	⊕⊕	+	N D	deciduous

\* For key to abbreviations and symbols, see end of Table 1.

Table 1.—continued.

Species	I E	I F	O F	H D	A I F	F H
<i>M. folgneri</i> Schneid.	—	⊕⊕	—~⊕⊕	—	++	
	—	—	⊕⊕	++	—	deciduous
<i>M. japonica</i> Dcne.	—	⊕⊕	—	+	++	
	—	—	⊕⊕	+	+	deciduous
<i>Aronia</i>						
<i>A. arbutifolia</i> Elliot	—	+~++	+~++	—	++	+
	—	+	++	++	++	++
<i>A. melanocarpa</i> Elliot	—	t~+	t~+	—~+	++	+
	—	t	++	++	++	++
<i>A. prunifolia</i> Rehder	—	+~++	t~++	—~+	(+)	+
	—	t	++	++	++	++
<i>Photinia</i>						
<i>P. davidsoniae</i> Rehd. et Wils.	+~++	+++	+	+	+++	+
	—	—	+	++	+	+
<i>P. glabra</i> Maxim.	—	—	—	—	(+)	—
	—	—	—	—	—	—
<i>P. integrifolia</i> Lindl.	+~++	+++	++	—	+++	N D
	—	—	—	++	+	++
<i>P. prunifolia</i> Lindl.	—~++	t	t	—	+	+
	—	—~++	—~+	+~++	—~++	+
<i>P. serratifolia</i> Kalkman	++	—	—	—	++	—
	—	—	—	—	—	+
<i>P. stenophylla</i> Hand.-Mazz.	+~++	—	—	—	(+)	—
	—	—	—	+	—	+
<i>P. wrightiana</i> Maxim.	—~+	t	t	—	—	—
	—	++	—	—	—	+
<i>Stranvaesia</i>						
<i>S. amphidoxa</i> Schneid.	—	++	++	++	++	++
	—	—	—	—	—	—
<i>S. davidiana</i> Dcne.	+	—	—	—	(+)	—
	—	—	—	—	—	—
<i>S. nussia</i> Dcne.	—~+	+++	—	—	+++	+
	—	—	—	—	—	—
<i>S. undulata</i> Dcne.	t	—	—	—	(+)	—
	—	—	—	—	—	—
<i>Heteromeles</i>						
<i>H. arbutifolia</i> Roem.	—	—	t~+	t~+	++	+~++
	—	—~+	+++	++	++	++

Table 1—continued.

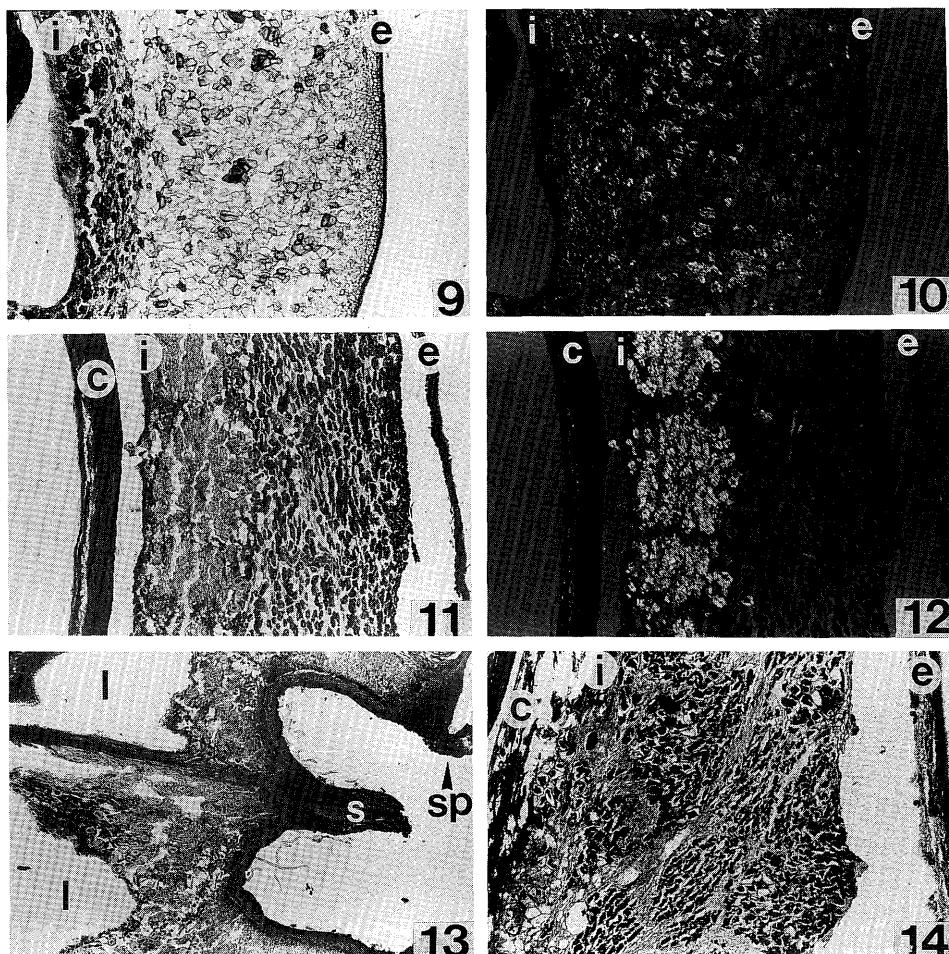
Species	I E	I F	O F	H D	A I F	F H
<i>Pourthiaeae</i>						
<i>P. arguta</i> DCNE.	—	(⊕)	⊕	—	—	+++
var. <i>salicifolia</i> Iketani et Ohashi	—	—	—	++	—	—
<i>P. beauverdiana</i> Hatusi	—	—	⊕	—	—	+++
var. <i>notabilis</i> Hatusi	— ~ +	—	⊕	—	—	⊕ ~ ++
<i>P. impressivena</i> Iketani et Ohashi	—	—	⊕	—	t	⊕
<i>P. villosa</i> DCNE.	—	—	⊕	—	—	+++ ~ ⊕
var. <i>parvifolia</i> Iketani et Ohashi	—	—	⊕	—	—	⊕
<i>Eriobotrya</i>						
<i>E. bengalensis</i> Hook. f.	t	++	++	— ~ +	++	++
	—	+	+	+	+	+
<i>E. cavaleriei</i> Rehder	—	++	++	— ~ t	++	+
	+	+	+	+	+	+
<i>E. deflexa</i> Nakai	—	—	—	—	+	+
	—	++	+	+	++	+
<i>E. fragrans</i> Champ.	—	++	++	—	++	+
<i>E. japonica</i> Lindl.	—	—	t	—	+	+
	—	++	t	++	++	+
<i>E. salwinensis</i> Hand.-Mazz.	—	+ ~ ++	+ ~ ++	—	++	+ ~ ++
	+	+ ~ ++	+ ~ ++	++	++	+
<i>Rhaphiolepis</i>						
<i>R. indica</i> Lindl.	—	+	++	+	++	deciduous
var. <i>umbellata</i> Ohashi	—	—	+	++	+	
<i>R. ferruginea</i> Metcalf	—	+	+	—	N D	deciduous
	—	+	+	++	N D	
<i>Chaenomeles</i>						
<i>C. speciosa</i> Nakai	—	++	—	++	++	deciduous
	—	—	—	+	N D	
<i>Pseudocydonia</i>						
<i>P. sinensis</i> Koehne	—	⊕	⊕	t	++	deciduous
	+	—	—	++	N D	

Table 1—continued.

Species	I E	I F	O F	H D	A I F	F H
<i>Cydonia</i>						
<i>C. oblonga</i> Mill.	—	⊕	⊕	—	++	not
	—	—	—~+	+	—	fleshy
<i>Docynia</i>						
<i>D. indica</i> Dcne.	++	⊕	⊕	+	+	N D
	—	+	+	++	+	N D
<i>Pyrus</i>						
<i>P. pyrifolia</i> Nakai	—	⊕	⊕⊕~+	+	+	
	—	+	+	++	+	deciduous
<i>Malus</i>						
<i>M. baccata</i> Desf.	N D	—	—	—	N D	
var. <i>sibirica</i> Schneid.	N D	++	—	+	N D	deciduous
<i>M. domestica</i> Borkh. 'AKANE'	++	—	—	—	—	not
	—	—	—	+	—	fleshy
<i>M. floribunda</i> Sieb.	++	+	—	—	N D	
	—	—	—	+	N D	deciduous
<i>M. prunifolia</i> Borkh.	++	—	—	—	+	not
	—	—	—	+	—	fleshy
<i>M. toringo</i> Vriese	+	—	—	—	—	not
	—	—	—	—	—	fleshy
<i>M. tschonoskii</i> Schneid.	++	⊕~++	⊕~++	+~++	++	not
	—	+	+	++	++	fleshy
<i>Amelanchier</i>						
<i>A. asiatica</i> Walp.	—	t ~+	+	+~++	+	+
	—	—	—	++	—	—
<i>A. sanguinea</i> DC.	—	t ~+	+	—	+	t
	—	—	t ~+	++	t	t
<i>A. spicata</i> C. Koch	—	—~+	—	—	+	+
	—	—	—	++	—	—
<i>Peraphyllum</i>						
<i>P. ramosissimum</i> Nutt.	—	t	t	—	+	N D
	—	—	—	+	+	N D

Abbreviations. IE: inner epidermis, IF: inner flesh, OF: outer flesh, HD: hypodermis, AIF: apical part of the inner flesh, FH: a portion of free hypanthium.

In each taxon, upper symbols indicate the distributional pattern of stone cells and lower symbols indicate that of pigment cells. The symbols correspond to those of Fig. 7 and Fig. 8. Columns with "ND" are not observed mainly due to bad preparation of samples.



Figs. 9–14. Fruit of subg. *Sorbus*, subg. *Torminalia* and subg. *Chamaemespilus* of *Sorbus*. Figs. 9, 10: *S. sambucifolia* (Ikemoto 1215). Longitudinal section.  $\times 19$ . Figs. 11–13: *S. terminalis* (from Bot. Gard. Vrije Univ.). Longitudinal section (Figs. 11, 12) and the apical part of the inner flesh and style (Fig. 13). The separation between epidermis and flesh is an artifact (Figs. 11, 12). Sepal is persistent but shriveled up (Fig. 13).  $\times 19$ . Fig. 14: *S. chamaemespilus* (from Jard. Bot. alpine "La Jaysinia"). Longitudinal section. The separation between epidermis and flesh is an artifact.  $\times 19$ . Figs. 10 and 12: same field as Figs. 9 and 11, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat, s: style, l: locule, sp: sepal.

the apical part of the inner flesh. Pigment cells are few in the inner flesh but rather many in the outer flesh. A portion of free hypanthium and sepals become fleshy except for the tip of sepals.

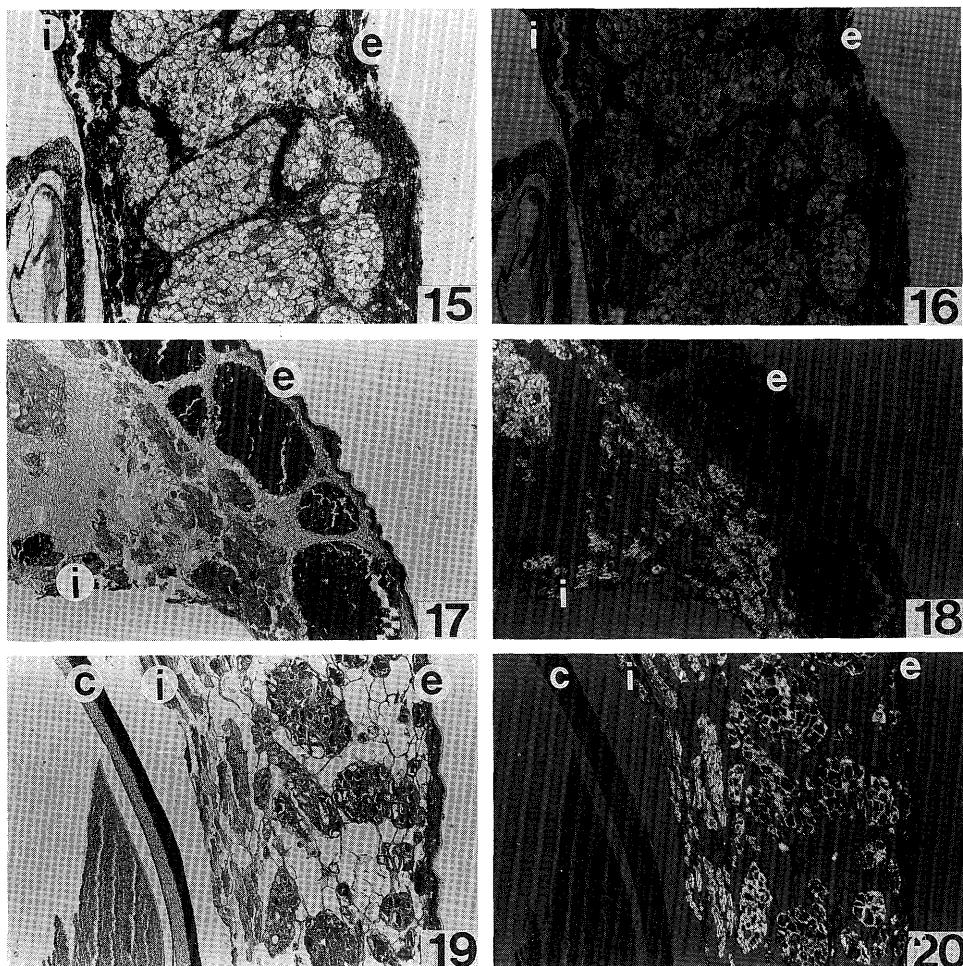
#### *Photinia* (Figs. 27–36)

Inner epidermis and neighboring several layers of cells are sclerified except for *Photinia glabra* (Fig. 31). The shape of these sclereids is isometric (Figs. 27, 33, 34) or radially elongated (Figs. 35, 36). Stone cells are usually absent or few in the

inner flesh, but in *P. davidsoniae* and *P. integrifolia* they appear densely (Figs. 29, 30). Stone cells are absent or few in the outer flesh, but they appear densely in *P. integrifolia*. Pigment cells are usually absent. The apical part of the inner flesh have no, a few or rather many stone cells. A portion of free hypanthium and sepals becomes fleshy except for the tip of sepals.

#### *Stranvaesia* (Figs. 37–40)

Inner epidermis is not sclerified (*S. amphidoxa*),



Figs. 15–20. Fruit of subg. Aria of *Sorbus*. Figs. 15, 16: *S. hayastana* (Karaprtjen s.n.). Longitudinal section.  $\times 19$ . Figs. 17, 18: *S. xanthoneura* (1980 Sino-American Exped. 719). Longitudinal section.  $\times 19$ . Figs. 19, 20: *S. lanata* (Kitamura s.n.). Longitudinal section.  $\times 19$ . Figs. 16, 18 and 20: same field as Figs. 15, 17 and 19, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat.

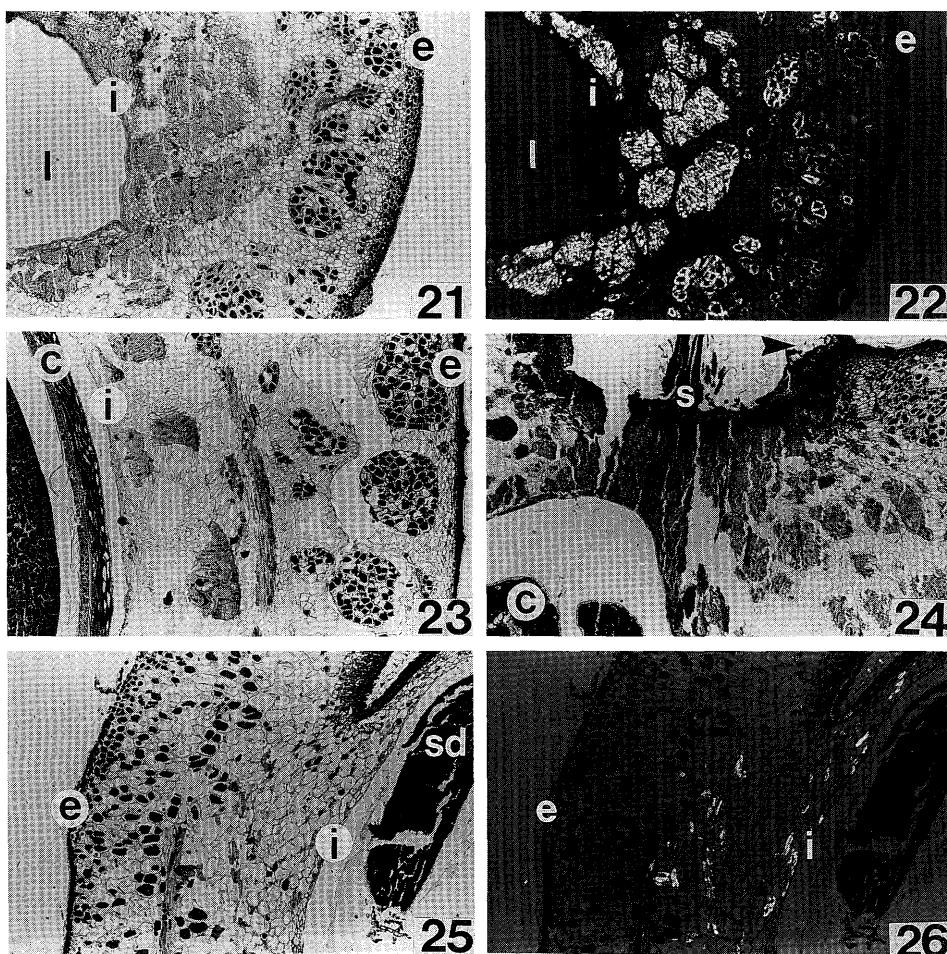
partly sclerified (*S. nussia*, *S. undulata*), or completely sclerified (*S. davidiana*). The shape of these sclereids is either isodiametric or radially elongated. Stone cells are usually absent or appear sparsely in the inner flesh, but in *S. amphidoxa* and *S. nussia* stone cells appear densely in the inner flesh. In the outer flesh stone cells are absent or appear sparsely, but in *S. amphidoxa* they appear densely. Pigment cells are usually absent. A portion of free hypanthium and sepals become fleshy except for the tip of sepals.

#### *Heteromeles* (Figs. 41, 42)

Inner epidermis is not sclerified. Stone cells are absent or appear sparsely in the flesh. Pigment cells appear densely in almost all part of the flesh. A portion of free hypanthium and sepals become fleshy except for the tip of sepals.

#### *Pourthiaeae* (Figs. 43–48)

Inner epidermis is not sclerified. Clusters of stone cells appear at about the middle part of the flesh. The size of each stone cell is not clearly larger than that of parenchymatous cell. Stone cells don't



Figs. 21–26. Fruit of *Micromelis* and *Aronia*. Figs. 21, 22: *M. alnifolia* (Ikeda 2016). Transverse section.  $\times 19$ . Figs. 23, 24: *M. japonica* (Ikeda 1663). Longitudinal section (Fig. 23) and the apical part of the inner flesh and style (Fig. 24). Arrow in Fig. 24 indicates the top of hypanthium after the falling of the free hypanthium and sepals.  $\times 19$ . Figs. 25, 26: *A. prunifolia* (Ikeda 2019). Longitudinal section.  $\times 19$ . Figs. 22 and 26: same field as Figs. 21 and 25, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat, s: style, sd: seed, l: locule.

appear in the other part of the flesh. Pigment cells are few or absent and do not appear in the clusters of stone cells. The apical part of the inner flesh usually has many stone cells. A portion of free hypanthium and sepals become fleshy except for the tip of sepals.

#### *Eriobotrya* (Figs. 49, 50)

Inner epidermis is not sclerified. Stone cells and pigment cells are absent or appear sparsely or rather densely in the inner flesh, outer flesh and the apical part of the inner flesh. A portion of free

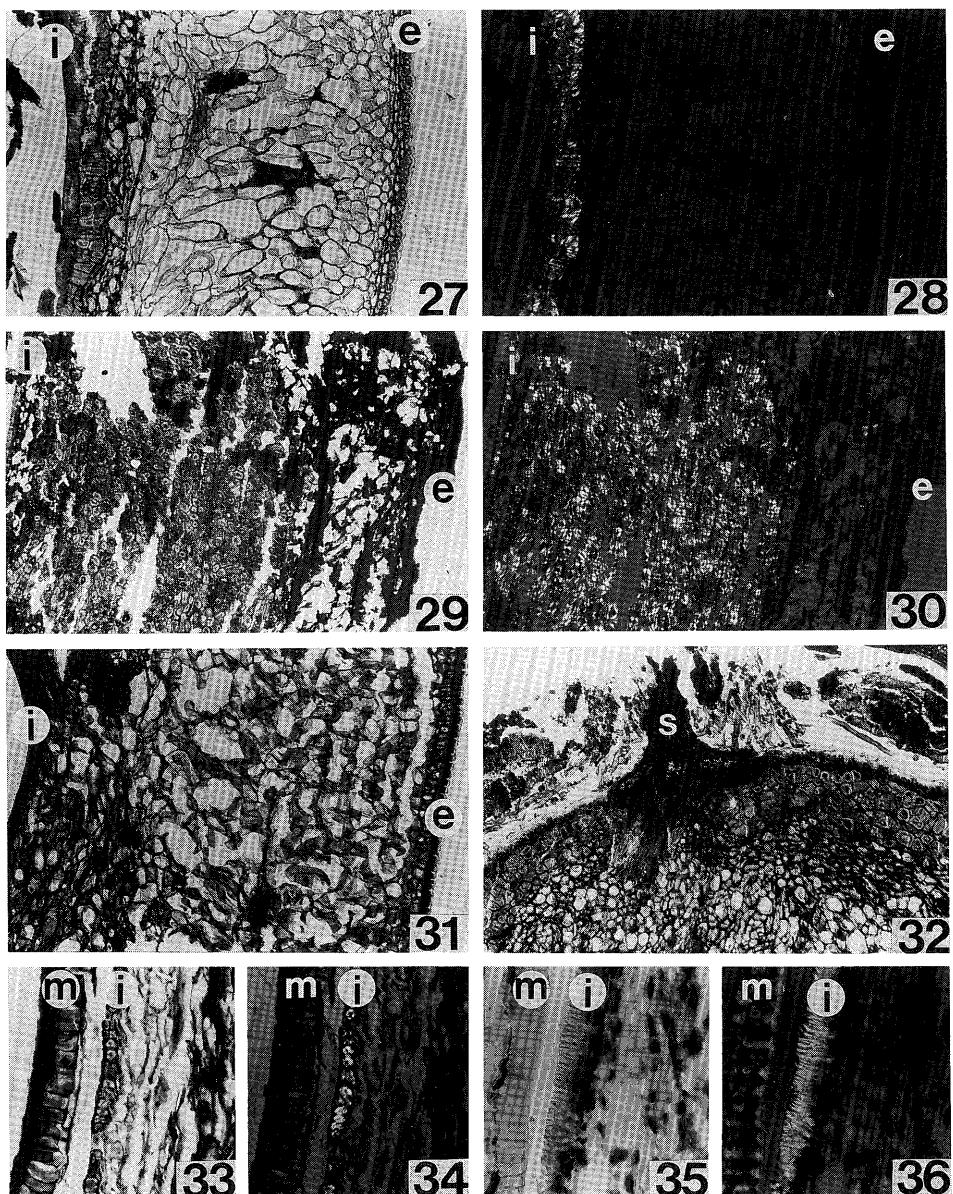
hypanthium usually becomes fleshy but sepals in some species don't.

#### *Rhaphiolepis* (Figs. 51, 52)

Inner epidermis is not sclerified. Stone cells and pigment cells are absent or appear sparsely in the inner flesh and outer flesh. The apical part of the inner flesh has many stone cells. A portion of free hypanthium and sepals fall off after anthesis.

#### *Chaenomeles* (Figs. 53–56)

Inner epidermis is not sclerified. Small clusters of stone cells appear rather densely near the dorsal



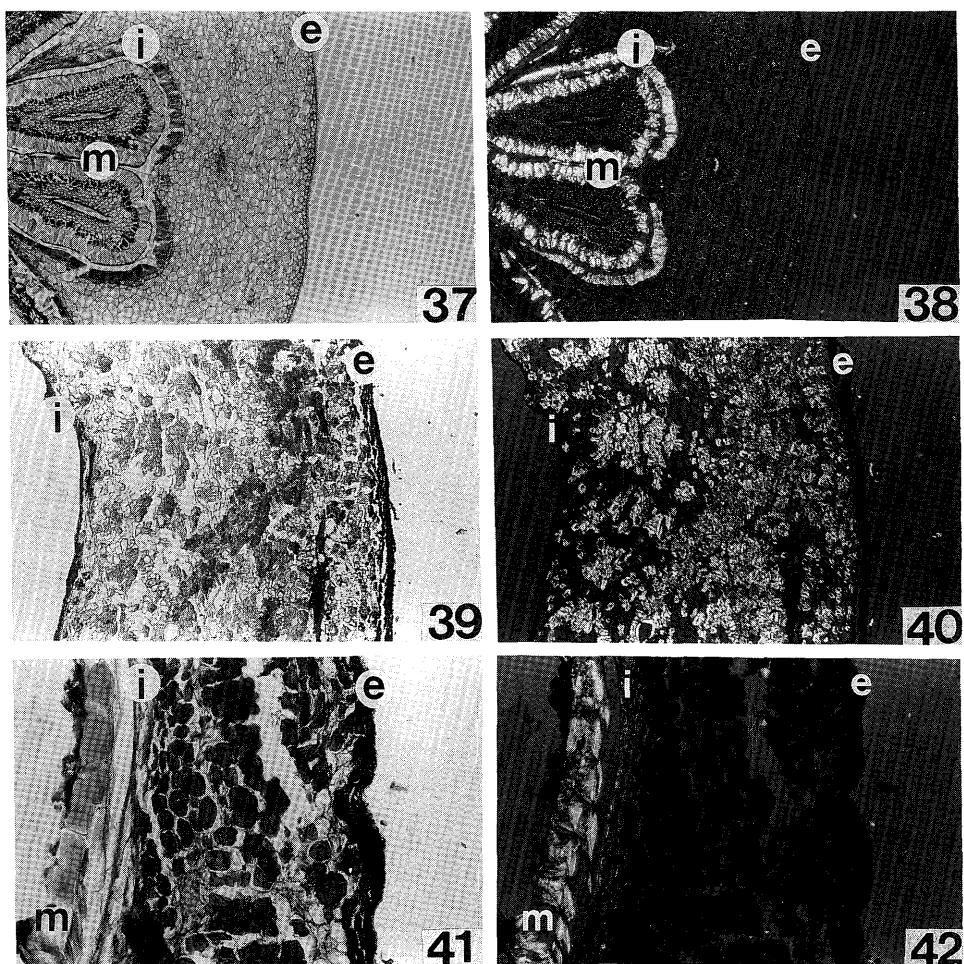
Figs. 27–36. Fruit of *Photinia*. Figs. 27, 28: *P. serratifolia* (Iketsu 2027). Longitudinal section.  $\times 45$ . Figs. 29, 30: *P. davidsoniae* (Tang 20660). Longitudinal section.  $\times 29$ . Fig. 31: *P. glabra* (Iketsu 1174). Longitudinal section.  $\times 45$ . Fig. 32: *P. serratifolia* (Iketsu 2027). The apical part of the inner flesh and style.  $\times 45$ . Figs. 33, 34: *P. stenophylla* (Tagawa et al. T514). Inner epidermis and neighboring cells.  $\times 88$ . Figs. 35, 36: *P. wrightiana* (Yamazaki 1675). Inner epidermis and neighboring cells.  $\times 88$ . Figs. 28, 30, 34 and 36: same field as Figs. 27, 29, 33 and 35, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, s: style, m: mucilaginous cell of the seed coat.

bundles of the ovary. Stone cells are absent from other parts of the inner flesh and outer flesh. Pigment cells and a few stone cells appear in the hypodermis. The apical part of the inner flesh has

many stone cells. A portion of free hypanthium and sepals fall off after anthesis.

#### *Pseudocydonia* (Figs. 57–60)

Inner epidermis is not sclerified. No stone cells

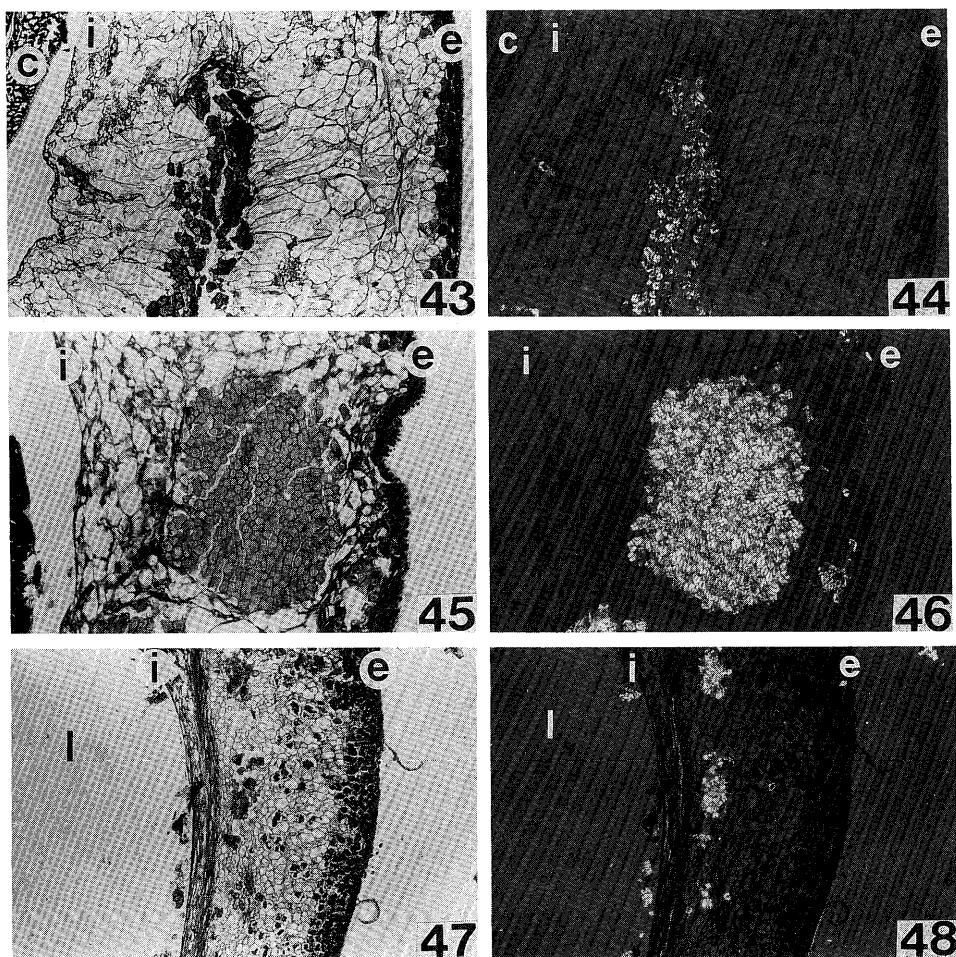


Figs. 37-42. Fruit of *Stranvaesia* and *Heteromeles*. Figs. 37, 38: *S. davidiana* (Ikeda 2026). Transverse section.  $\times 19$ . Figs. 39, 40: *S. amphidoxa* (Teng 90474). Longitudinal section.  $\times 19$ . Figs. 41, 42: *H. arbifolia* (Hiroe 10044).  $\times 49$ . Figs. 38, 40 and 42: same field as Figs. 37, 39 and 41, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, m: mucilaginous cell of the seed coat.

are found in the inner part of the inner flesh, i.e. the area inner than the dorsal bundles of the carpel. But outside of this area clusters of stone cells appear in almost all part of the inner flesh and outer flesh. These clusters are large and appear densely in the inner part and decrease toward outside of the fruit. Pigment cells appear only in the hypodermis. The apical part of the inner flesh has many stone cells. A portion of free hypanthium and sepals fall off after anthesis.

*Cydonia* (Figs. 61-64)

Inner epidermis is not sclerified. No stone cells are found in the inner part of the inner flesh, i.e. the area inner than the dorsal bundles of the carpel. But outside of this area, clusters of stone cells appear in almost all the parts of the inner flesh and outer flesh. The size and distributional pattern of these clusters are similar to those of *Pseudocydonia*. Pigment cells appear only in the hypodermis. The apical part of the inner flesh has many stone cells. A portion of free hypanthium and sepals are persistent in the mature fruit but doesn't



Figs. 43–48. Fruit of *Pourthiaeae*. Figs. 43, 44: *P. villosa* (Iketani 1662). Transverse section.  $\times 29$ . Figs. 45, 46: *P. impressivena* (Taam 146). Longitudinal section.  $\times 49$ . Figs. 47, 48: *P. villosa* var. *parvifolia* (Young 219). Longitudinal section.  $\times 19$ . Figs. 44, 46 and 48: same field as Figs. 43, 45 and 47, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat, l: locule.

become fleshy.

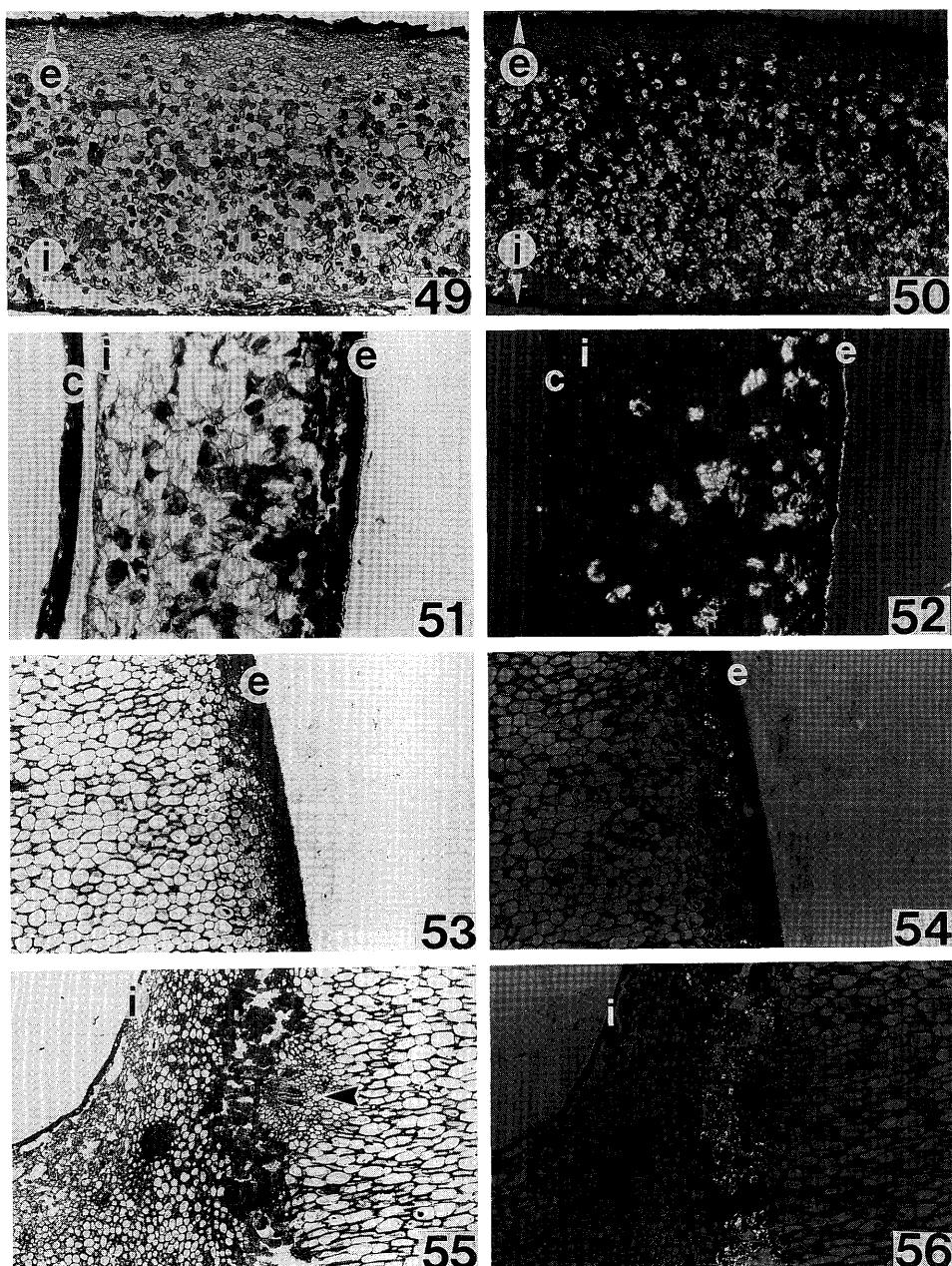
#### *Docynia* (Figs. 65–68)

Inner epidermis and neighboring cells are sclerified. The shape of these sclereids is isometric. Clusters of stone cells appear rather densely in the inner flesh and outer flesh. The size and density of these clusters are not different among the part of the flesh. The apical part of the inner flesh has many stone cells. Pigment cells appear sparsely in the whole part of flesh. A portion of free hypanthium and sepals become fleshy in the mature fruit except for the tip of sepals.

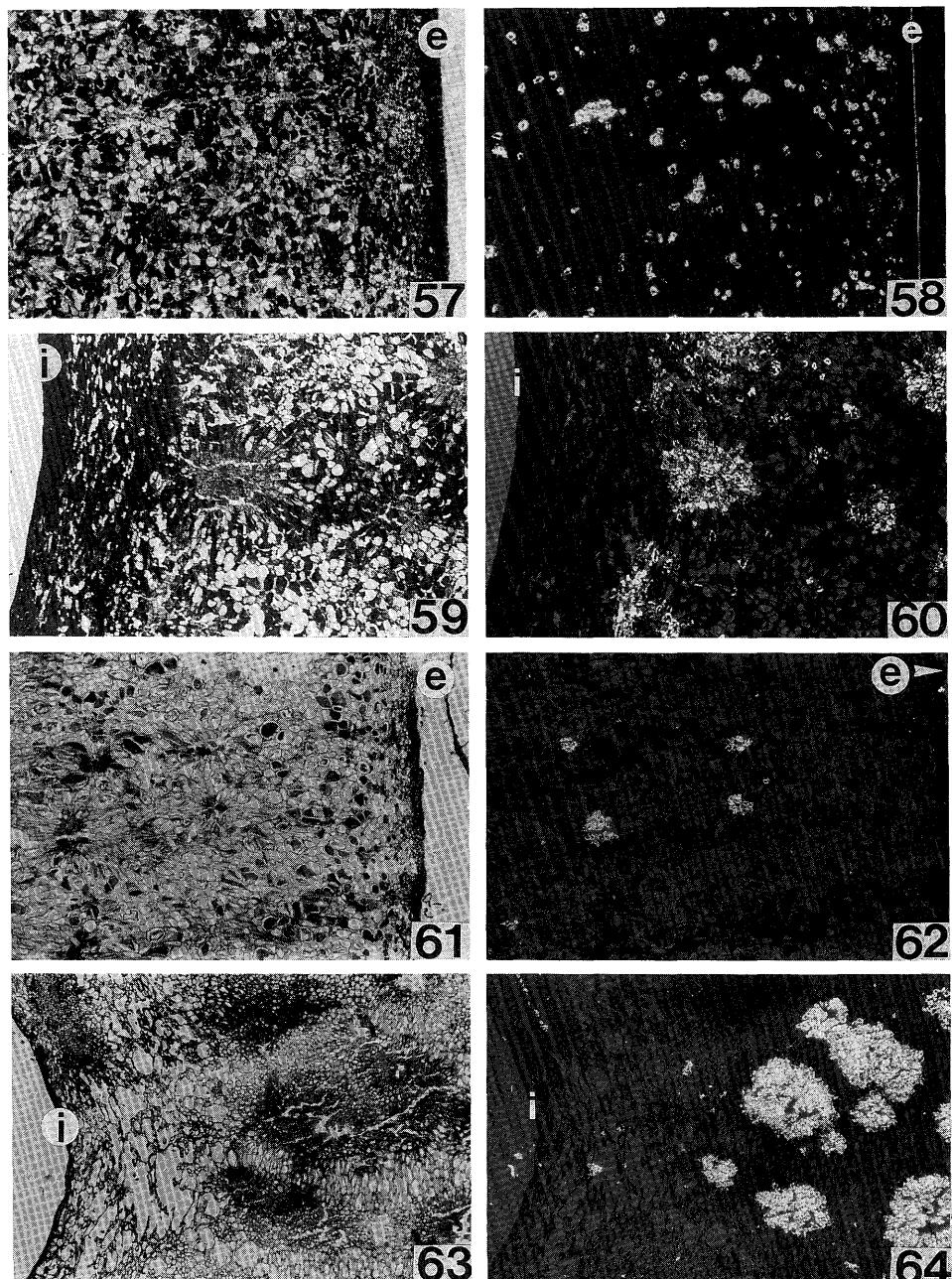
#### *Pyrus* (Figs. 69–72)

Inner epidermis is not sclerified. Clusters of stone cells appear in the inner flesh and outer flesh. The size and distributional pattern of these clusters are similar to those of *Pseudocydonia*. Pigment cells appear sparsely in the flesh. The apical part of the inner flesh has many stone cells. Species examined is *Pyrus pyrifolia* in this study, but almost same results of observations are reported by MacDaniels (1940), Sterling (1954), and Roth (1977) on *P. communis*.

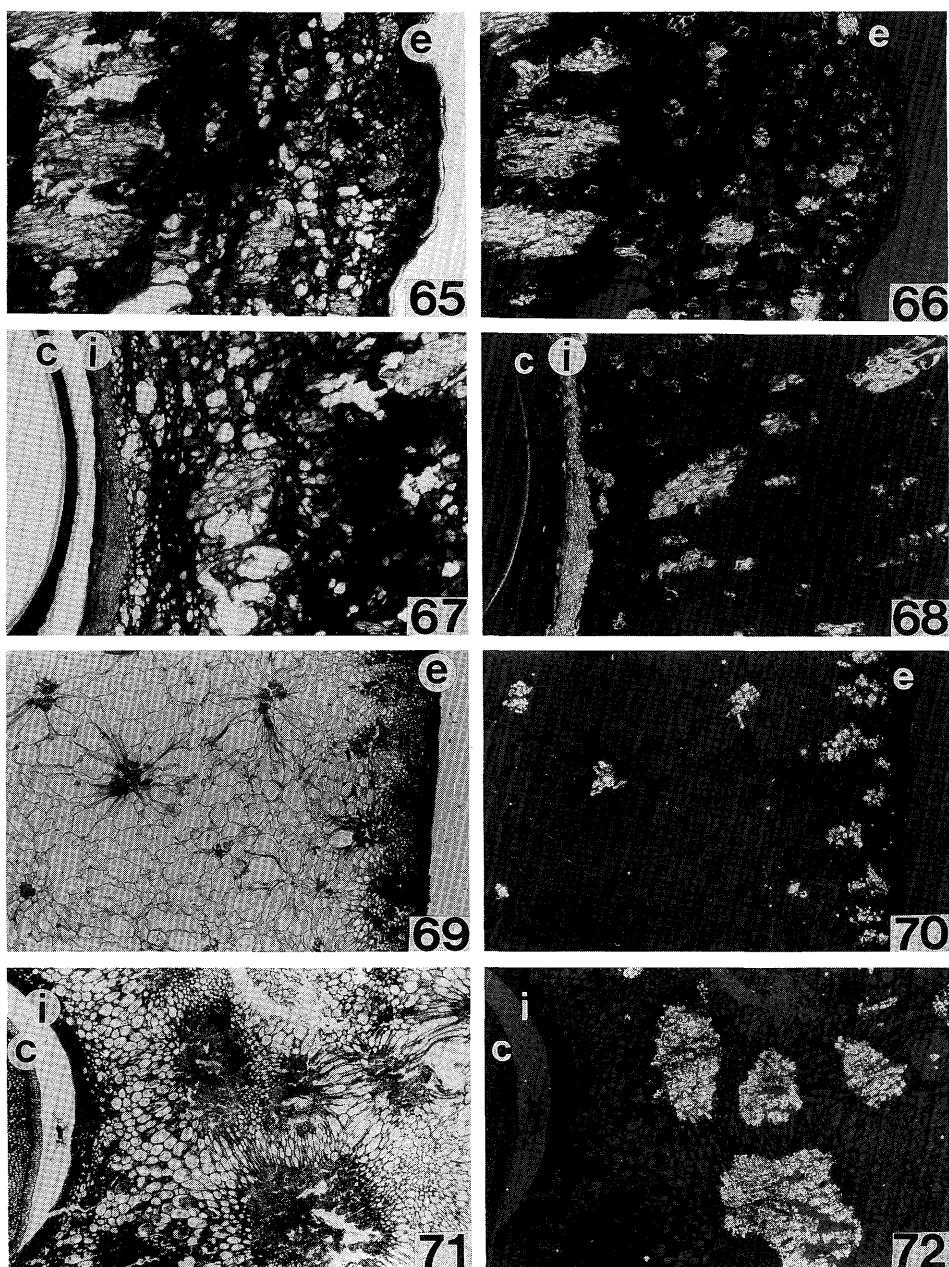
#### *Malus* (Figs. 73–80)



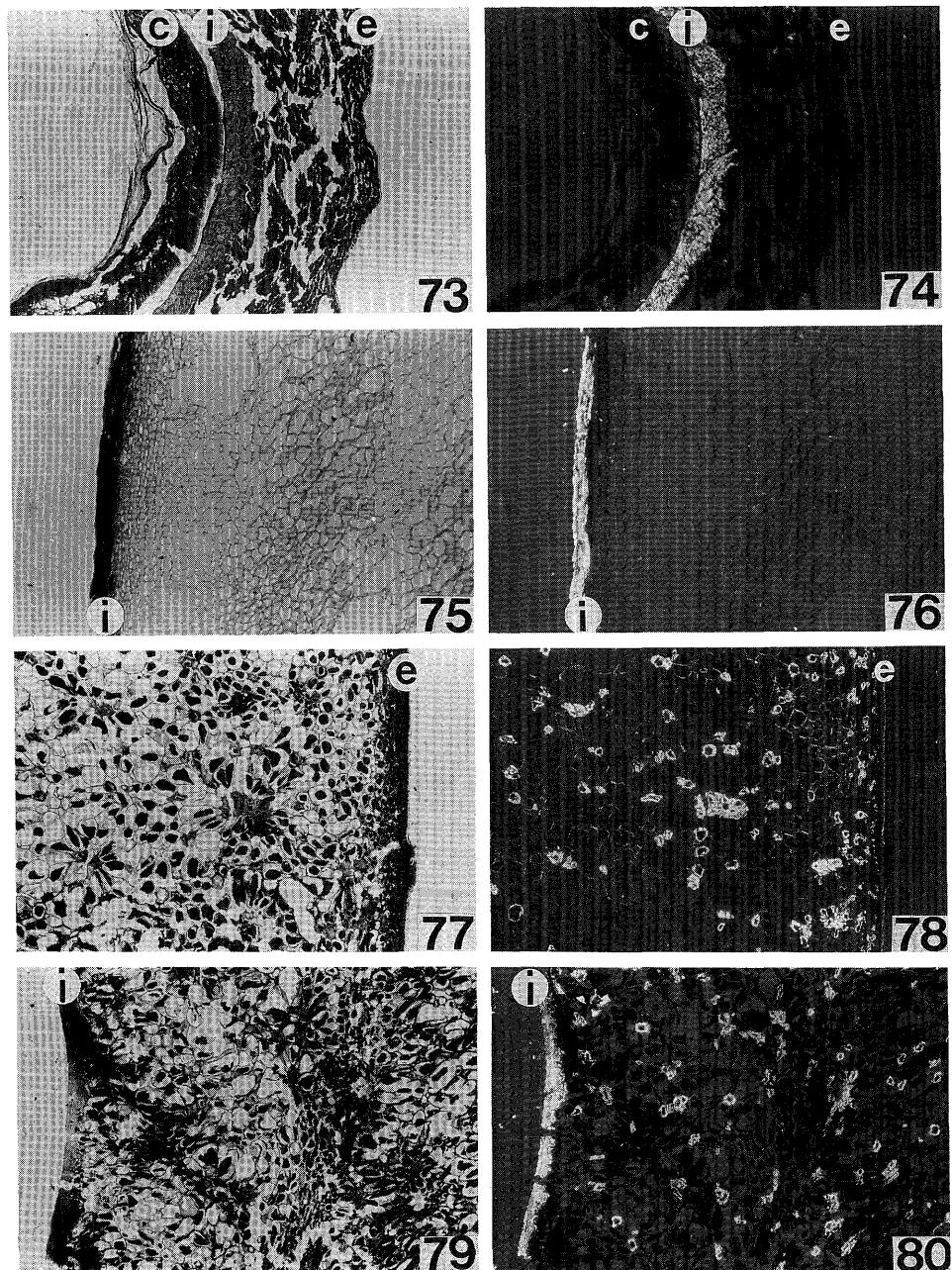
Figs. 49–56. Fruit of *Eriobotrya*, *Rhaphiolepis* and *Chaenomeles*. Figs. 49, 50: *E. salwinensis* (Kanai et al. s.n.). Transverse section.  $\times 19$ . Figs. 51, 52: *R. indica* (Iketani 2047). Longitudinal section.  $\times 49$ . Figs. 53–56: *C. speciosa* (Iketani 2363). Figs. 53, 54: Transverse section through outer part of fruit. Figs. 55, 56: Transverse section through inner part of fruit. Arrow indicates the dorsal bundle of the carpel.  $\times 19$ . Figs. 50, 52, 54 and 56: same field as Figs. 49, 51, 53 and 55, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat.



Figs. 57–64. Transverse sections through fruit of *Pseudocydonia* and *Cydonia*. Figs. 57–60: *P. sinensis* (Ikeda 2014). Outer part (Figs. 57, 58) and inner part (Figs. 59, 60).  $\times 19$ . Figs. 61–64: *C. oblonga* (Purchased, Sendai). Outer part (Figs. 61, 62) and inner part (Figs. 63, 64).  $\times 19$ . Figs. 58, 60, 62 and 64: same field as Figs. 57, 59, 61 and 63, respectively, seen in crossed polarized light. e: epidermis; i: inner epidermis.



Figs. 65–72. Transverse sections through fruit of *Docynia* and *Pyrus*. Figs. 65–68: *D. indica* (Hara et al. 6301816). Outer part (Figs. 65, 66) and inner part (Figs. 67, 68).  $\times 19$ . Figs. 69–72: *P. pyrifolia* (Ikeda 1699). Outer part (Figs. 69, 70) and inner part (Figs. 71, 72).  $\times 19$ . Figs. 66, 68, 70 and 72: same field as Figs. 65, 67, 69 and 71, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat.



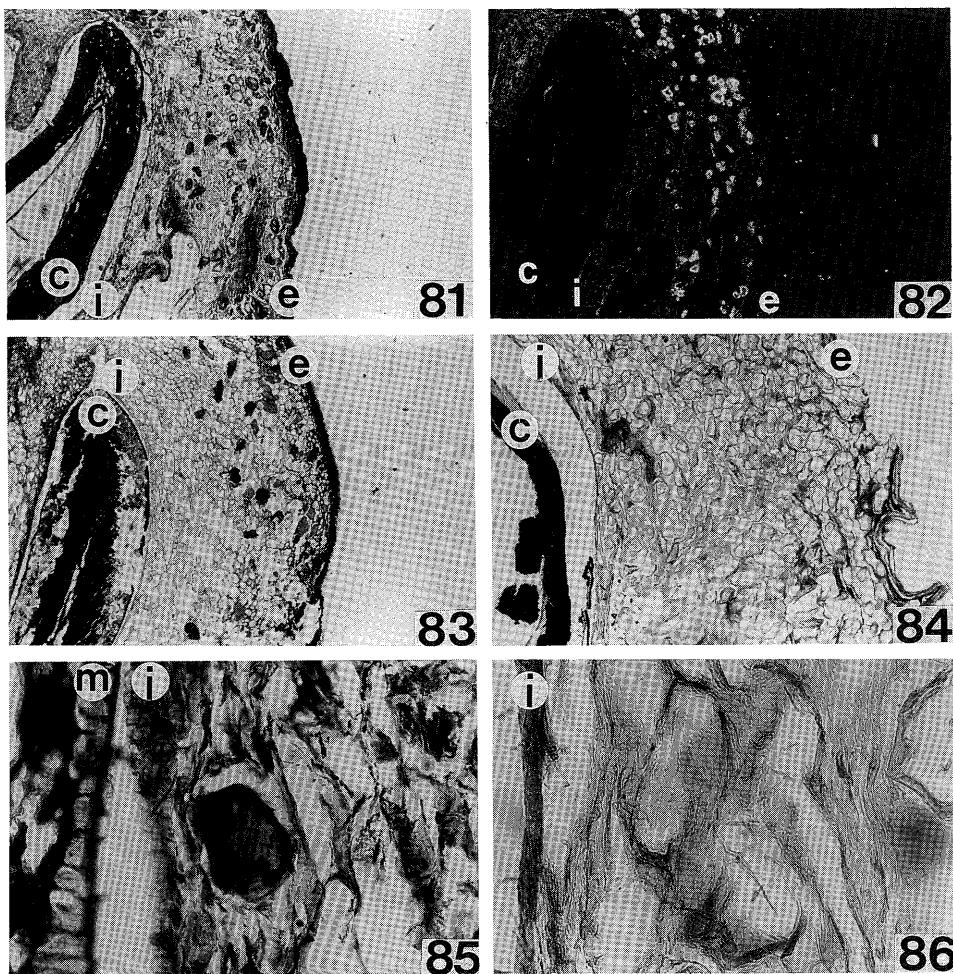
Figs. 73–80. Transverse sections through fruit of *Malus*. Figs. 73, 74: *M. floribunda* (from Nat. Bot. Gard., Glasnevin).  $\times 29$ . Figs. 75, 76: *M. domestica* 'Akane' (Purchased, Sendai). Inner part.  $\times 19$ . Figs. 77–80: *M. tschonoskii* (Ikeda 2155). Outer part (Figs. 77, 78) and inner part (Figs. 79, 80).  $\times 19$ . Figs. 74, 76, 78 and 80: same field as Figs. 73, 75, 77 and 79, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat.

Inner epidermis and the neighboring cells are sclerified and usually the shape of these sclereids is radially elongated. Stone cells are absent or only a few in the flesh except for *Malus tschonoskii*, in which small clusters of stone cells appear sparsely or rather densely in the flesh. Pigment cells are absent or appear rarely in the flesh except for *M. tschonoskii*, in which there are a few pigment cells in the flesh. A portion of free hypanthium and sepals fall off after anthesis or they are persistent in the mature fruit.

#### *Amelanchier* (Figs. 81–83, 85)

Inner epidermis is not sclerified. Stone cells appear sparsely or rather densely in the inner and outer flesh. Pigment cells appear only in the hypodermis. The apical part of the inner flesh has no, a few or rather many stone cells. A portion of free hypanthium and sepals become fleshy except for the tip of sepals. Olson and Steeves (1982) reported fruit structure of *A. alnifolia* and their results are almost same as our observation.

#### *Peraphyllum* (Figs. 84, 86)



Figs. 81–86. Fruit of *Amelanchier* and *Peraphyllum*. Figs. 81, 82, 85: *A. sanguinea* (from Concer. Jard. Bot. Nancy). Longitudinal section (Figs. 81, 82).  $\times 19$ . Inner epidermis and neighboring cells (Fig. 85).  $\times 190$ . Fig. 83: *A. asiatica* (Ikeda 1966). Longitudinal section.  $\times 19$ . Figs. 84, 86: *P. ramosissimum* (Matsumura s.n.). Longitudinal section (Fig. 84).  $\times 19$ . Inner epidermis and neighboring cells (Fig. 86).  $\times 190$ . Fig. 82: same field as Fig. 81, respectively, seen in crossed polarized light. e: epidermis, i: inner epidermis, c: seed coat, m: mucilaginous cell of the seed coat.

Inner epidermis is not sclerified. Stone cells are absent or rare in the flesh. Pigment cells appear only in the hypodermis. The apical part of the inner flesh has stone cells only at the under part of styles. A portion of free hypanthium and sepals become fleshy except for the tip of sepals.

*Malacomeles* and subgenus Cormus of *Sorbus* were not examined in this study. Kovanda (1961) described the fruit structure of Cormus as follows: "the pulp is homogeneous with numerous stone cells, and the endocarp is very thin and membranous". From this description, we think that the pulp of Cormus is homogeneous like that of subgenus Sorbus of *Sorbus*, and that the inner epidermis and neighboring cells are not sclerified. And we surmise that the pulp structure of *Malacomeles* is similar to *Amelanchier* and *Peraphyllum* on the basis of the description of Robertson et al. (1991).

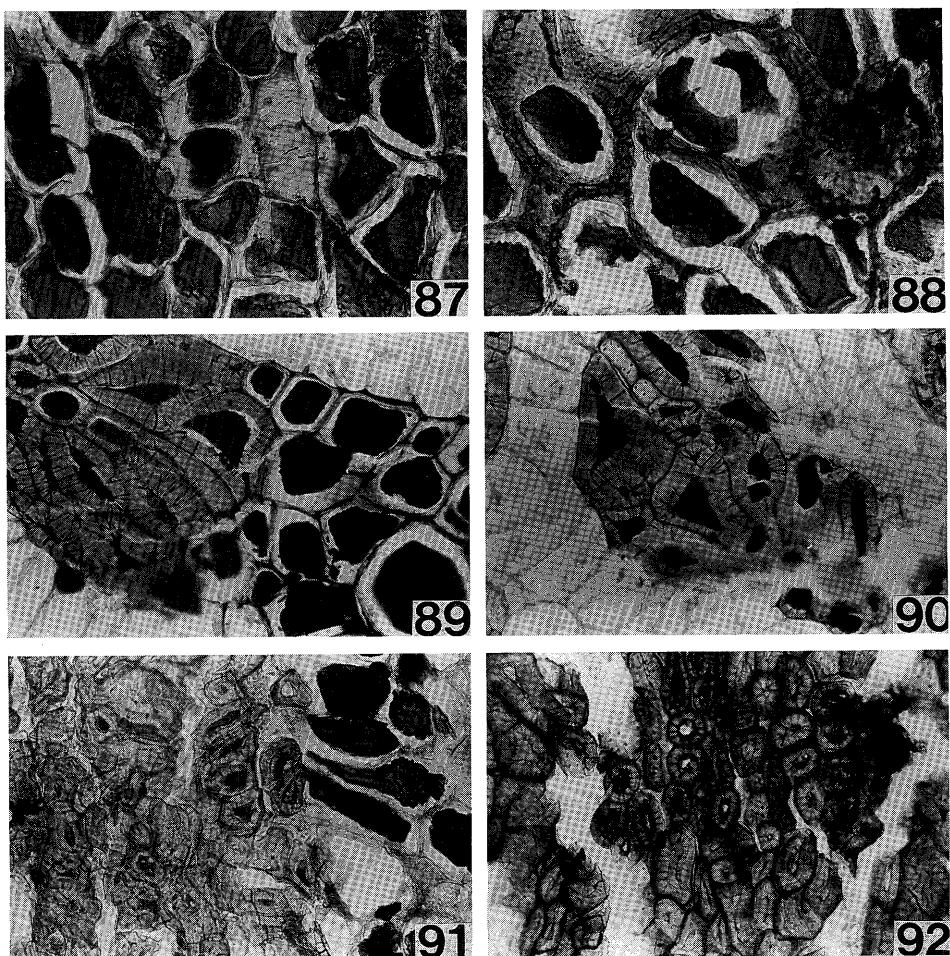
### Discussion

Decaisne (1874) first described the heterogeneous pulp of subgenus Aria of *Sorbus*. He reported that it is similar to that of *Pourthiae* and *Micromeles*. Kovanda (1961) reinvestigated this structure with the Chekoslovakian species of Aria and described the heterogeneous pulp as consisting of basic parenchymatous cells and large sized cells. He stated that sclereids are not found in this heterogeneous pulp in the species he examined except inter-subgeneric hybrids. But Gabrielian (1958) observed clusters of pigment cells and stone cells in the pulp of Caucasian species of Aria. In the present study, a few stone cells were observed in clusters in the inner flesh in *Sorbus hayastana* and *S. kusnetzovii*; both species are distributed from the Caucasus to eastern Europe. In the Asiatic species of Aria stone cells and sclerenchymatous pigment cells are present in the inner flesh or throughout the flesh.

Main components of clusters in *Micromeles* are mainly pigment cells in the outer flesh and stone cells in the inner flesh. But there are continuous forms intermediate between these two cell types. Vacuoles of stone cells in the inner flesh are usually rich in pigment (Fig. 90) and pigment cells in the outer flesh have thickened walls (Fig. 89). The flesh of the Asian species of Aria is similar to that of *Micromeles* (Figs. 87, 88), but the difference between the outer flesh and the inner flesh is somewhat obscure. The flesh of the Caucasian and European species of Aria and Chamaemespilus have few or no stone cells, and most or all cells in the clusters are large sized pigment cells or parenchymatous cells without pigments. Therefore, variation of the heterogeneous pulp is morphologically and geographically continuous among these three taxa, and we think this character is homologous in them.

Systematic relationships among *Micromeles* and the subgenera of *Sorbus* are still obscure (Challice and Kovanda 1978). Challice and Kovanda (1978) proposed two phylogenetic schemes for the origin of the subgenera of *Sorbus* mainly based on the distribution of phenolic compounds. In their schemes, Torminalia evolved from primitive *Crataegus*, and Aria and Chamaemespilus developed from Torminalia (Fig. 4 in Challice and Kovanda 1978), or, otherwise, Aria, Chamaemespilus, and Torminalia evolved independently from primitive *Crataegus* (Fig. 5 in Challice and Kovanda 1978). In both schemes, *Sorbus* (sens. str.) and Cormus derived from Aria.

It must be possible to suppose either of two hypotheses when we follow their schemes; i.e., the heterogeneous pulp resulted through parallel evolution, or the heterogeneous pulp is a primitive state that have already appeared in primitive *Crataegus* from which the pulp structure of Torminalia evolved. In both hypotheses the pulp structure of



Figs. 87–92. Stone cells and pigment cells of *Sorbus* subg. *Aria*, subg. *Torminalia*, *Micromeles*, and *Pourthiaeae*.  
 Fig. 87: *S. cuspidata* (Stainton et al. 8619). Pigment cells in the outer flesh. Cell walls are slightly thickened and lignified.  
 Fig. 88: Ibid. Pigment cells of the inner flesh. Cell walls are fairly thickened and lignified. Fig. 89: *M. japonica* (Iketani 1663). Pigment cells and stone cells of the outer flesh. Stone cells are filled with pigment. Cell wall of the pigment cells are thickened and lignified. Fig. 90: Ibid. Stone cells of the inner flesh. Stone cells are rich in pigment.  
 Fig. 91: *S. torminalis* (from Bot. Gard. Vrije Univ.). Pigment cells and stone cells of the inner flesh. Stone cells are filled with pigment. The size of the stone cells is not larger than that of other cells. Cell wall of the pigment cells is not thickened nor lignified. Fig. 92: *P. impressivena* (Taam 146). Stone cells. They do not contain pigment and they do not differ in size from other cells. All  $\times 140$ .

*Sorbus* and *Cormus* are supposed to have evolved from that of *Aria*. In this case we must suppose reversal evolution from the heterogeneous pulp to the homogeneous pulp. Challice and Kovanda (1978) assumed the relationship of *Torminalia* and *Crataegus* by the resemblance of structure of the innermost part of the pulp, because they considered that of *Torminalia* as thick and tough. But

actually, the inner epidermis and neighboring cells are not sclerenchymatous, and clusters of stone cells are distributed only in the outer part of the inner flesh. This structure is also unique in the subfamily, and we also think this as a derived state. Therefore, it is difficult to assume a close relationship between *Crataegus* and *Torminalia*. Whether the evolution of pulp is from the *Torminalia* type

to the Aria type or *vice versa* is also difficult to assume. Phylogenetic schemes of Challice and Kovanda (1978) are not supported from our results on the pulp structure.

*Micromeles* is usually treated as congeneric with *Sorbus* (Hedlund 1901, Rehder 1940, Hutchinson 1964, McAllister 1986, Phipps et al. 1990), but sometimes treated as a separate genus (Decaisne 1874, Koehne 1890, Kalkman 1973, Kovanda and Challice 1981). Kovanda and Challice (1981) postulated the close relationship of *Micromeles* and *Rhaphiolepis* in spite of many morphological differences. They denied the relationship between *Micromeles* and Aria because free part of hypanthium and sepals never fall off after anthesis in the latter. But this character appears in many genera of Maloideae. Especially in *Malus* and *Pyrus*, both persistent and deciduous forms appear within one genus. So, in this family, this character is not necessarily a synapomorphy and it can be assumed that *Micromeles* evolved from an ancestral type of Himalayan Aria species which had an almost inferior ovary and fused styles at the base. *Micromeles* and Aria may be monophyletic and we agree with the treatment of Aria including *Micromeles* (Robertson et al. 1991). Chamaemespilus may have evolved from the ancestor of Aria through loss of sclerification of the large sized cells. Non discoid homogamous flower and other distinctive characters of Chamaemespilus (Robertson et al. 1991) may be autoapomorphies.

The pulp structure of *Pourthiaeae* shows a distinct difference from that of the Aria type. In *Pourthiaeae* stone cells become clusters, but pigment cells or sclerenchymatous pigment cells do not appear in these clusters, and the size of the stone cells is not much larger than the parenchyma (Fig. 92). So, the structure is not the same as the heterogeneous pulp of the Aria type. On the other hand the pulp structure of *Aronia* is homogeneous, and

is not similar to that of *Pourthiaeae*. So, while *Aronia* is congeneric with *Photinia* as stated by Robertson et al. (1991), *Aronia* may have independently evolved from the ancestor of *Photinia*, and is not monophyletic with *Pourthiaeae*.

*Photinia* and *Stranvaesia* display great diversity as regards to the distribution of sclerenchymatous cells in the pulp structure. This variation can be conveniently classified into the following three types: 1) Almost the entire inner flesh becomes sclerenchymatous and in some cases the outer flesh also becomes sclerenchymatous (*P. davidsoniae*, Figs. 29, 30; *P. integrifolia*; *S. amphidoxa*, Figs. 39, 40; and *S. nussia*). 2) Only the inner epidermis and neighboring cells become sclerified (*P. prunifolia*; *P. serratifolia*, Figs. 27, 28; *P. stenophylla*, Figs. 34, 35; *P. wrightiana*, Figs. 35, 36; *S. davidiana*, Figs. 37, 38; and *S. undulata*). 3) Few or no stone cells are present in the pulp and inner epidermis (*P. glabra*, Fig. 31). We think these variations have resulted from parallel evolution of loss of stone cells, and do not indicate heterogeneity of genera. The fruit of *Stranvaesia* is often described as dehiscent at maturity, and, in this character it is separated from *Photinia* (Rehder 1940, Hutchinson 1964). Kalkman (1973) denied the dehiscence of the fruit of *Stranvaesia*, and we have also observed no dehiscence in *S. davidiana* cultivated in Japan. In fact, there are no structures such as an abscission layer that indicate the dehiscence in fruits of *Stranvaesia*. Consequently, these two genera cannot be distinguished by the fruit structure, nor by any other characters. So, we agree with the treatment of *Stranvaesia* included in *Photinia* (Kalkman 1973, Robertson et al. 1991).

*Chaenomeles*, *Pseudocydonia*, *Docynia*, and *Cydonia* are recognized by Hutchinson (1964), Yü (1974, 1984), and Kalkman (1988) as closely related to each other, or the former three genera are recognized by Koehne (1891) and Robertson et al.

(1991) as related to *Malus* while the last *Cydonia* to *Pyrus*. In fruit anatomy, *Chaenomeles* differs from the others in the distribution of stone cells in the pulp. This observation agrees with the description of Weber (1964), who pointed out that *Chaenomeles* is similar to the most of *Malus* in having few or no stone cells in most part of the pulp. However, *Chaenomeles* has many stone cells around the dorsal bundles of the carrels, and in this respect it differs from *Malus*.

*Docynia* differs from the others in having a sclerenchymatous inner epidermis and neighboring cells. *Malus* has also the same character; in particular, *M. tschonoskii* is very similar to *Docynia* in having clusters of stone cells in the pulp. *Malus* sect. *Docyniopsis*, where *M. tschonoskii* belongs, and sect. *Eriolobus* have many stone cells in the pulp (Rehder 1940). From this point these two sections were treated as distinct genera (Koidzumi 1934, Robertson et al. 1991) or as members of *Docynia* (Schneider 1906).

*Pyrus* and *Malus* have been recognized as closely related and sometimes they were united into one genus (Fernand 1947, Robertson 1974). In the pulp structure, *Pyrus* is similar to *M. tschonoskii*, but *Pyrus* does not have a sclerenchymatous inner epidermis. *Pyrus* is rather similar to *Cydonia* and *Pseudocydonia* in anatomical characters of the fruit.

*Amelanchier* and *Peraphyllum* are considered to be related through several characters (Jones 1945, Robertson et al. 1991). They have similar characteristics in the pulp structure.

**Evolution of the pulp structure** There are two convincing hypotheses on the origin of Maloideae. One is that the ancestor of Maloideae is an allopolyploid between a spiraeoid-ancestor and a amygaldaloid-ancestor (Sax 1932; Stebbins 1950; Challice 1974, 1981; Phipps et al. 1991). The other is that only a spiraeoid ancestor is the original

rootstock of Maloideae (Gladkova 1972). From the above hypotheses, the following hypotheses of evolutionary trends in the fruit in Maloideae may be deduced.

One supposed ancestral type may be an achene derived from a follicle through the indehiscence of the ventral suture (Fig. 93: A). All parts of the carpels became sclerified at maturity of the fruit. Then the hypanthium became fleshy and enlarged, enclosing the carpels. The fruit of *Pyracantha* is the most primitive in the Maloideae, consisting of five almost apocarpous carpels fused to a fleshy calyx only half way from the base (Fig. 93: B). The fruit of Crataegeae is more primitive than that of Sorbeae. Robertson et al. (1991) denied to distinguish the tribes in the Maloideae, and they inferred that *Crataegus*, *Mespilus*, *Hesperomeles*, and *Osteomeles* are closely related to *Pyrus* and *Malus*, and that *Cotoneaster* and *Pyracantha* are similar to *Sorbus* and *Photinia*. Phipps et al. (1991) inferred that the very hard pyrenes of *Crataegus* and others have been derived from a hardening core (that corresponds to our sclerified inner epidermis and neighboring cells in this paper) like that of *Malus* rather than a soft pyrene like that of *Cotoneaster*. But so far as we observed, the carpels of the fruit of the Crataegeae consist of sclerified isometric cells (e. g., Figs. 3–6) and no histological differences were observed between the soft and the hard pyrenes of their sense. We could recognize a difference of thickness of carpel between both pyrenes. So we think it is not impossible to think an evolution from soft pyrene to hard pyrene. If adopting the premise of evolution from “hardening core” to “hard pyrene” by Phipps et al. (1991), we must think such a reverse evolution of carpels as once sclerified to fleshy then fleshy to sclerified, so far as thinking spiraeoid follicle as the ancestral type. Therefore we think that Crataegeae may be a paraphyletic group

sharing the sclerified carpels of the fruit as a symplesiomorphy, and that Sorbeae may be an monophyletic group sharing incompletely or not sclerified carpels of the fruit as a synapomorphy. Among Sorbeae, the most primitive fruits are those in some species of *Photinia* and *Stranvaesia* in which almost all parts of the inner flesh and inner epidermis remain sclerenchymatous (Fig. 93: C).

The density of stone cells in the flesh were diminished from these fruits. Then clusters of stone cells became scattered in the flesh. The size of the clusters further became smaller, and solitary stone cells became scattered in the flesh or they are nearly absent (Fig. 93: D). The pulp structure of the *Pourthiaeae* type (Fig. 93: E), the *Micromeles* type (Fig. 93: F), and the *Torminalia* type (Fig. 93: G) are considered to be apomorphic state. Inner epidermis and neighboring cells are supposed to have evolved from sclerenchymatous to fleshy as well as the flesh, but they may have evolved relatively independently from the flesh. In many cases the loss of stone cells in the flesh was correlated with that of inner epidermis and neighboring cells, but in some case, the flesh has no stone cells as against sclerenchymatous inner epidermis (e.g., *Malus*).

The other possibility for the ancestral type is a drupe. Only the innermost part of the carpels became sclerenchymatous in drupes. But if a drupe were adopted as the ancestral type, it must have evolved from an achene. In this case, reverse evolution is assumed in the carpels of the Crataegeae. Even if we accept that a amygdaloid-ancestor took part in the origin of the Maloideae, we can assume a capsule as in *Exochorda*, which, as suggested by Goldblatt (1976), should be transferred to the Amygdaloideae, as the ancestral fruit type in that subfamily, which assumes that a drupe was not necessarily the primitive type.

Kalkman (1988) performed a cladistic analysis

of Rosaceae. In the cladogram he considers the most plausible (Fig. 1 in Kalkman 1988), the Maloideae (Maleae and *Cydonia* group as Kalkman's operational units) forms a monophyletic group with Osmaroniae and Kerriae, and a synapomorphy of this group is the fleshy or juicy pericarp. In this case, reverse evolution must be assumed also for the evolution of the fruit of the Crataegeae. In Kerriae the fruit of *Neveusia* is a drupe, but that of *Kerria* is an achene, so the same assumption is needed.

In comparing the two hypotheses, the first is the more preferable from the principle of parsimony (Wiley 1981). Therefore, we hypothesize evolutionary trends of the fruit of Maloideae as in figure 93.

**Relationship of the genera of Sorbeae** The conventional system of Maloideae dividing it into two tribes, Crataegeae and Sorbeae, has not been convincingly proved yet. But, as discussed above, we think Crataegeae a paraphyletic group and Sorbeae an monophyletic group. In the Sorbeae the following three groups are evidently inferred as monophyletic from respective characteristics that are considered to be synapomorphies: 1) *Amelanchier*, *Peraphyllum*, and *Malacomeles* having false septa in the fruit; 2) subgenera *Aria* and *Chamaemespilus* of *Sorbus* and *Micromeles* having heterogeneous pulp structure; and 3) *Cydonia*, *Pseudocydonia*, and *Chaenomeles* having multiovulate carpels. In the last group, loss of the clusters of the stone cells and fusion of floral organ, i.e., adnation of carpels to the hypanthium and connation among carpels and styles, may have been correlative occurred. So, *Cydonia* may be the most plesiomorphic, but *Pseudocydonia* may be intermediate. *Chaenomeles* must be the most apomorphic. *Chaenomeles* is considered to be related to *Malus* by apparent similarity of the structure of fruit (Koehne 1891, Robertson et al.

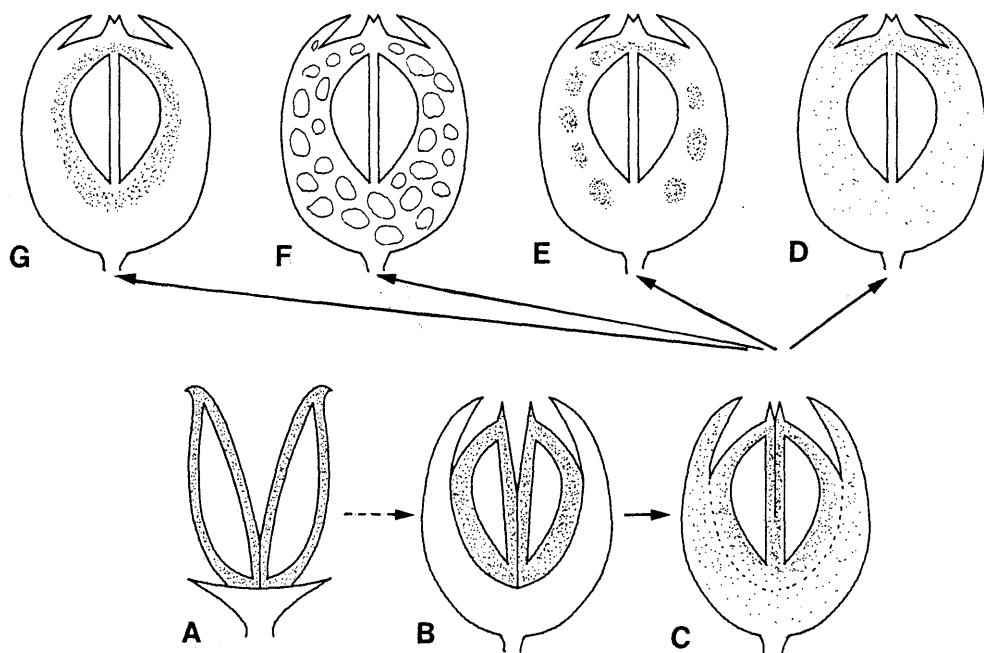


Fig. 93. Inferred evolutionary trends in the fruit of Sorbeae. A: supposed ancestral type, B: most primitive type in Maloideae (e.g., *Pyracantha*), C: primitive type in Sorbeae (e.g., *Photinia*, *Stranvaesia*), D: derived type, E: derived type (*Pourthiaeae*), F: derived type (e.g., *Micromeles*), G: derived type (*Sorbus* subg. *Torminalia*). Black dots represent sclerenchymatous parts. Irregular-shaped circles in F represent clusters of large sized cells. For further detailed explanation, see text.

1991). However, we cannot support this view based on the anatomical differences. Relationship of *Docynia* to other genera is still obscure. *Docynia* has three to ten ovules per locule (Robertson et al. 1991) against *Chaenomeles* and others having much more. As described above, the anatomical structure of the fruit of *Docynia* is similar to *Malus* especially to sect. *Docyniopsis* (and maybe to sect. *Eriolobus*). The similarity of the flavonoid chemistry of *Docynia* and *Docyniopsis* of *Malus* was reported by Williams (1982). We think that *Docynia* and *Docyniopsis* are closely related, but the similarity of the pulp structure of sclerenchymatous inner epidermis is inferred as plesiomorphy, so the monophyly of *Docynia* and *Docyniopsis* has not been proved. *Pyrus* and *Cydonia* have a very similar structure of the fruit. *Pyrus* may have been branched from the ancestor of *Cydonia* before the latter acquired the

multiovulate character.

*Pourthiaeae* and subgenus *Torminalia* of *Sorbus* have very distinctive characters inferred as autoapomorphies respectively. *Pourthiaeae* is clearly distinct and it has evidently evolved from *Photinia*. To *Torminalia* the most closely related group in the Sorbeae may be *Aria* though there are many differences between both taxa. *Torminalia* is considered to be differentiated from the ancestor of *Aria* before the latter acquired the heterogeneous pulp.

To infer more detailed and complete phylogenetic scheme in this tribe is very difficult. As pointed out by Phipps et al. (1991), the evolution of the genera of Maloideae has a possibility of polychotomous (reticulate) origin. In this situation normal methodology of reconstruction of phylogeny (e.g., parsimony method) is not applicable without excluding the taxa of hybrid origin before

analyzing (Hull 1979, Funk 1981). It is necessary to make clear the existence and pattern of reticulate evolution of genera to infer the phylogeny of Maloideae in the future study.

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#### Endnote

1) Present address: Division of Breeding, Fruit Tree Research Station, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, 305 Japan.  
農林水産省果樹試験場 305 茨城県つくば市藤本  
2-1.

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## 要 旨

バラ科はふつう4亜科に分類され、その1つであるナシ亜科 Maloideae は約23属1,110種を含み、サンザシ連 Crataegeae とナナカマド連 Sorbeae とに分類されている (Phipps et al. 1990). Decaisne (1874) はナシ亜科の果実を初めて解剖学的に体系的に研究し、不均質な構造の果肉をもつ群のあることを記録した。しかし、この解剖学的な差異についてはその後植物学的にはほとんど研究されずに残されていて、Gabrielian (1958) と Kovanda (1961) がヨーロッパのナナカマド属を研究した際に、果実の解剖学的形質がナナカマド属の分類形質として有用であることを報告したに過ぎない。バラ科では果実の形質は重要な分類形質とされており、特にナシ亜科は梨果（ナシ状果）をもつことが主要な特色である。そこで、われわれはナシ亜科における果実の解剖学的形質を再検討し、この形質がナシ亜科の分類形質として有用であるか否かを判定するために、ナシ亜科の22属74種（そのうちナナカマド連は17属62種、サンザシ連は7属12種）について果実の解剖学的形態を調べた。この論文は、ナナカマド連の果実の解剖学的構造を記載し、この形質の進化傾向を考察し、その結果に基づいてナナカマド連に含まれる属の系統関係を推定したものである。

観察の結果、ナナカマド連では果実の解剖学的形質が属のレベルで異なることが判明した。多くの属では果肉は主として柔細胞よりなり、少数の石細胞が散在するかあるいは石細胞が存在しないという均質な構造を示した。これに対し、いくつかの属では果肉は柔細胞、石細胞、および色素細

胞よりなる不均質な構造を示した。リンゴ属 *Malus* ドキニア属 *Docynia*、カナメモチ属 *Photinia* の一部の種、およびニイタカカマツカ属 *Stranvaesia* の一部の種を除き、ナナカマド連では内果皮は厚壁化しないことを明らかにした。

これらの観察結果を、サンザシ連やバラ科の他の亜科の果実と比較して、ナシ亜科における果実の形質進化を推定した。ナシ亜科においては、心皮の全体が骨化するサンザシ連の果実はそのようにならないナナカマド連の果実よりも原始的であると推定した。ナナカマド連においては、多くの属で果肉中の石細胞が失われる方向に進化したと推定した。また、カマツカ属 *Pourthiae* では石細胞が果肉の中央部に塊状に集合して分布するという特徴を示し、アズキナシ属 *Micromeles* およびナナカマド属 *Aria* 亜属と *Chamaemespilus* 亜属では周囲の細胞より大きな色素細胞および石細胞またはそのうちのどちらかが塊状に集合して果肉の全体に分布するという特徴を示し、ナナカマド属 *Torminalia* 亜属では石細胞が塊状に集合して果肉内層に分布するという特徴を示した。これらの特徴はそれぞれ特殊化した進化であり、固有派生形質であると推定された。

## Appendix

### Materials examined and voucher specimens

Fresh materials with collecting data and voucher herbarium specimens are listed with an asterisk (\*) after the collection number. When no voucher specimens are available, collecting data are listed. Dried materials were collected from herbarium specimens listed here and from botanical gardens or institutes through seed exchange programs. Voucher specimens are preserved in the following herbaria: Biological Institute, Faculty of Science, Tohoku University (TUS); Botanical Gardens, Faculty of Science, Tohoku University (TUSG); University Museum, University of Tokyo (TI);

National Science Museum, Tokyo (TNS); Department of Botany, Faculty of Science, Kyoto University (KYO); and Liberty Hyde Bailey Hortorium, Cornell University (BH).

*Sorbus* L. subg. *Sorbus*

*S. commixta* Hedlund: Japan, Hokkaido, Mt. Kariba, 3 Aug. 1984, H. Hoshi et al. 1164\* (TUS). In the campus of the Faculty of Science, Tohoku University, cultivated, 2 Oct. 1985, H. Iketani 1729\* (TUS).

*S. esserteauiana* Koehne: In the Royal Horticultural Society Garden, England, cultivated, F.G. Meyer 3180 (BH).

*S. gracilis* (Sieb. et Zucc.) K. Koch: Japan, Yamanashi Pref., Yamanakako-mura. 10 Oct. 1985, H. Iketani 1979\* (TUS).

*S. matsumurana* (Makino) Koehne: Japan, Yamanashi Pref., Mt. Kitadake, 14 Oct. 1985, H. Iketani 993\* (TUS).

*S. pohuashanensis* (Hance) Hedlund: In the Royal Horticultural Society Garden, England, cultivated, F.G. Meyer 3432 (BH).

*S. sambucifolia* (Cham. et Schlecht.) Roemer: Japan, Yamanashi Pref., Mt. Kitadake. 14 Oct. 1985, H. Iketani 1215\* (TUS).

*S. scalaris* Koehne: Cultivated in Windsor Great Park, Collector unknown (BH).

*Sorbus* L. subg. *Torminalia* (DC.) K. Koch (= *Torminalis* Medik.)

*S. torminalis* (L.) Crantz: Botanical Garden, Vrije Universiteit, Netherlands, in 1984. Hortus Botanicus Camerinensis, Universita del Studi, Italy, in 1985.

*Sorbus* L. subg. *Chamaemespilus* (Medik.) K. Koch

*S. chamaemespilus* (L.) Crantz: Jardin Botanique Alpine "La Jaysinia", Samoens, France, in 1985.

*Sorbus* L. subg. *Aria* (Pers.) Beck

*S. cuspidata* (Spach) Hedlund: Nepal, Annapurna Himal., Modi Khola, Stainton, Sykes, and Williams 8619 (TI).

*S. hayastana* Gabrielian: USSR, ArmSSR; 25 Oct. 1958, R. Karaprtjen s.n., (BH).

*S. kusnetzovii* Zinserl.: USSR, ArmSSR, Daral'egis, Alazsko'e ushchel'je, 14 Oct. 1959, E. Gabrielian s.n., (BH).

*S. lanata* (Don) K. Koch: Afghanistan, Nuristan, Kushtaki to Pronz, 4 Aug. 1955, S. Kitamura s.n. (KYO).

*S. xanthoneura* Rehder: China, W. Hubei, Shennongjia Forest, 7 Sept. 1980, 1980 Sino-American Expedition No. 719 (KYO).

*Micromeles* Decaisne

*M. alnifolia* (Sieb. et Zucc.) K. Koch: In the campus of Tohoku University, cultivated, 1 Nov. 1985, H. Iketani 2016\* (TUS).

*M. caloneura* Stapf: China, W. Hubei, Shennongjia Forest, 8 Sept. 1980, 1980 Sino-American Expedition No. 753 (KYO).

*M. corymbifera* (Miq.) Kalkman: N. Thailand, Prov. Chiang Mai, C.F. von Beusekom and C. Phengklai 2425 (KYO).

*M. folgneri* Schneider: China, Kuling along Mt. Slope, 25 July 1928, C.Y. Chiao 18696 (BH). China, 13 July 1928, W.P. Fang 2177 (TNS). China, W. Hubei, Shennongjia Forest, 11 Sept. 1980, 1980 Sino-American Expedition No. 1008 (KYO). National Botanic Garden, Glasnevin, Dublin, in 1985.

*M. japonica* Decaisne: Japan, Miyagi Pref., Sendai Aobayama, 30 Oct. 1984, H. Iketani 1663\* (TUS).

*Aronia* Medikus

*A. arbutifolia* (L.) Elliot: T.R. Duke 8100 (TNS). Hortus Botanicus, Vrije Universiteit, in 1985.

*A. melanocarpa* (Michx.) Elliot: Botanic Garden of the University of Ferburg, BRD, in

1984.

*A. prunifolia* (Marsh.) Rehder: In the Aritaki Arboretum, Koshigaya, Saitama Pref., Japan, cultivated, 15 Nov. 1985, H. Iketani 2019\* (TUS).

*Photinia* Lindley

*P. davidsoniae* Rehder et Wilson: China, 2–30 Nov. 1932, W.T. Tsang 20660 (TI).

*P. glabra* (Thunb.) Maxim.: In the Matsugaoka Park, Taira, Iwaki, Fukushima Pref., Japan, cultivated, 4 Jan. 1987, J. Iketsu 1174\* (TUS).

*P. integrifolia* Lindley: Nepal, near Kathmandu, Sheopuri Lekh, Stainton, Sykes and Williams 6928 (TI).

*P. prunifolia* Lindley: China, Gungdong, Dinghusha, G.Q. Ding and K.L. Shi 1656, (TUS). Hongkong, Victoria Park, 5 Jan. 1964, H. Hara and S. Kurosawa s.n. (TI).

*P. serratifolia* (Desf.) Kalkman: In the Botanical Garden, Faculty of Science, University of Tokyo, cultivated, 20 Nov. 1985, H. Iketani 2027\* (TUS).

*P. stenophylla* Hand.-Mazz.: Thailand, M. Tagawa, K. Iwatsuki and N. Fukuoka T514 (KYO).

*P. wrightiana* Maxim.: Japan, Ryuku, Isl. Kumejima, Gushikawasan, T. Yamazaki 1675 (TUSG).

*Stranvaesia* Lindley

*S. amphidoxa* Schneider: China Kweichow, S.W. Teng 90474 (KYO).

*S. davidiana* Decaisne: In the Botanical Garden, Faculty of Science, University of Tokyo, cultivated, 20 Nov. 1985, H. Iketani 2026\* (TUS).

*S. nussia* (D. Don) Don: Nepal, Kathmandu District, D. H. Nicolson 2719 (TI).

*S. undulata* Decaisne: Botanic Garden, University of Oxford, in 1985.

*Heteromeles* Roemer

*H. arbutifolia* (Ait.) Roemer: M. Hiroe 10044, 22 Oct. 1955, (TNS). California, 1875, Y.R. Vasey s.n., (TI) Research Division, L.A. State and County Arboretum, in 1985.

*Pourthiaeae* Decaisne

*P. arguta* (Lindl.) Decne. var. *salicifolia* (Decne.) Iketani et Ohashi: Thailand, Prov. Chaiyaphum, Ban Nam Phrom, R. Geesink, T. Hattin, and K.C. Phengklai 6888 (KYO).

*P. beauverdiana* (Schneid.) Hatusima: China, Kwantung, Tinghushuan, K. S. Chow et al. 78003 (TUS).

——— var. *notabilis* (Schn.) Hatusima: Formosa Kirairei-Asahi, E. Matsuda 280, ut *P. kudoi* (TI). Botanic Garden of University of Oxford, in 1984. China, Guangzhonm, Guangdog, H.G. Yip 260 (TUS). Taiwan, Taihoku, Sinten, K. Odashima 13666 (TI), ut *Photinia benthamina*.

*P. impressivena* (Hayata) Iketani et Ohashi: China, Kwangtong, Sinfung District, Y.W. Taam 146, ut *Photinia euphlebia* Merr. et Chun. (KYO).

*P. villosa* (Thunb.) Decne.: Japan, Miyagi Pref., Sendai, Aobayama, 29 Oct. 1984, H. Iketani 1662\* (TUS). Japan, Yamanashi Pref., Aokigahara, 16 Oct. 1983, H. Iketani 1248\* (TUS). Japan, Miyagi Pref., Sendai, Aobayama, 2 Nov. 1985, H. Iketani 1665\* (TUS).

——— var. *parvifolia* (Pritz.) Iketani et Ohashi: Taiwan, Taipei Co., Shih-tung, K.C. Young 219 (TUS). Taiwan, Mt. Daiton, T. Sato 326, ut *Photinia kankoensis* (TI). China, Kwangtong, T.M. Tsui 638, ut *P. subumbellata* R. et W. (TI)

*Eriobotrya* Lindley

*E. bengalensis* (Roxb.) Hooker f.: S. W. Thailand, Prov. Kanchanaburi, Geesink and Phengkahl 6178 (KYO).

*E. cavaleriei* (Lévl.) Rehder: China, Kwantung Sin-fung district, Y.W. Taam 305 (KYO).

*E. deflexa* (Hemsl.) Nakai: Taiwan, Nantou Co., Y.F. Chen 3481 (TUS).

*E. fragrans* Champ.: China, Kwantung, south of Linchow, T.M. Tsui 614 (TI).

*E. japonica* (Thunb.) Lindley: In a private garden, Kawauchi, Sendai, Japan, cultivated, on 6 Aug. 1986\*.

*E. salwinensis* Hand.-Mazz.: Nepal, Godawari-Phulchoki, 23 June 1967, H. Kanai et al. s.n. (TI).

#### *Rhaphiolepis* Lindley

*R. indica* (L.) Lindl. ex Ker var. *umbellata* (Thunb. ex Murray) Ohashi: In the Botanical Garden, Faculty of Science, Tohoku University, cultivated, 22 Dec. 1986, H. Iketani 2047\* (TUS).

*R. ferruginea* Metcalf: China, Kwantung, Sin-fung district, Y.W. Taam 167 (KYO).

#### *Chaenomeles* Lindley

*C. speciosa* (Sweet) Nakai: In a private garden, Aobayama, Sendai, Japan, cultivated, 7 Sept 1986, H. Iketani 2363\* (TUS). In a private garden, Ouchi, Akita, Japan, cultivated, on 15 Sept. 1986\*.

#### *Pseudocydonia* Schneider

*P. sinensis* (Thourin) Koehne: In the medical plants garden of the Faculty of Pharmacology, Tohoku University, cultivated, 5 Nov. 1985 and 3 Nov. 1986, H. Iketani 2014\* (TUS).

#### *Cydonia* Miller

*C. oblonga* Miller: Purchased at a market in Sendai city, Japan, on 22 Oct. 1986\*. Purchased at a market in Sendai city, Japan, on 28 Oct. 1986\*.

#### *Docynia* Decaisne

*D. indica* Decaisne: Sikkim, Yoksan, H. Hara et al. 6459 (TI). East Nepal, Dumban, Taplejung, H. Hara et al. 6301816 (TI).

#### *Pyrus* L.

*P. pyrifolia* (Burm. f.) Nakai: Aobayama, Sendai, Japan, cultivated, 15 Sept. 1985, H. Iketani 1699\* (TUS).

#### *Malus* Miller

*M. baccata* (L.) Desf. var. *sibirica* (Maxim.) Schneider: Korea, Inter Nansen et Ariyjo, 7 Sept. 1902, T. Uchiyama s.n. (TUS).

*M. floribunda* Siebold: National Botanic Garden, Glasnevin, in 1985.

*M. prunifolia* (Willd.) Borkh.: In the medical plants garden of the Faculty of Pharmacology, Tohoku University, cultivated, 3 Nov. 1985, H. Iketani 2013\* (TUS).

*M. domestica* Borkh. 'Akane': Purchased at a market in Sendai, on 29 Sept. 1986\*.

*M. toringo* (Sieb.) Sieb. ex Vriese: In the Botanical Garden, Faculty of Science, Tohoku University, cultivated, on 14 Sept. 1986\*.

*M. tschonoskii* (Maxim.) Schneider: Japan, Miyagi, Sendai, Aobayama, in the campus of the Faculty of Pharmacology, Tohoku University, 3 Nov. 1985, H. Iketani 2155\* (TUS). Japan, Miyagi, Sendai, Aobayama, in the Botanical Garden, Faculty of Science, Tohoku University, 9 Nov. 1985, H. Iketani 1661\* (TUS).

#### *Amelanchier* Medikus

*A. asiatica* (Sieb. et Zucc.) Endl. ex Walp.: In the experimental garden of the Biological Institute, Faculty of Science, Tohoku University, cultivated, 1 Oct. 1985, Japan, H. Iketani 1966\* (TUS).

*A. sanguinea* (Pursh) DC.: Conservatoire et Jardin botanique de Nancy.

*A. spicata* (Lam.) K. Koch: Botanisch Garten, Munchen-Nymphenburg.

#### *Peraphyllum* Nutall

*P. ramossissimum* Nutt.: U.S.A., Colorado, 1963, Y. Matsumura s.n., (KYO).

*Mespilus* L.

*M. germanicus* L.: Botanisk Museum, Hage  
Univ. Bergen.

*Dichotomanthes* Kurz.

*D. tristaniaecarpa* Kurz.: Hortus Botanicus  
Instituti Botanici nom V. L. Komarovii.

*Cotoneaster* Medikus

*C. frigidus* Wall. ex Lindl.: National Botanic  
Garden, Glasnevin, Dublin.

*C. horizontalis* Decne.: In the medical plants  
garden of the Faculty of Pharmacology,  
Tohoku University, cultivated, 27 Oct. 1986, H.  
Iketani 2045\* (TUS).

*C. moupinensis* Franch.: National Botanic  
Garden, Glasnevin, Dublin.

*C. rhystidophyllus* Rehd. et Wils.: National  
Botanic Garden, Glasnevin, Dublin.

*Pyrantha* Roemer

*P. crenulata* (D. Don) Roemer: In the Botanical

Garden, Faculty of Science, Tohoku University,  
cultivated, 2 Oct. 1985, H. Iketani 2048\* (TUS).

*Crataegus* L.

*C. monogyna* Jacq.: In the Botanical Garden,  
Faculty of Science, Tohoku University,  
cultivated, 2 Oct. 1985, H. Iketani 1715\* (TUS).

*Hesperomeles* Lindley

*H. cuneata* Lindl. Peru, 14 Nov. 1965, F.  
Maekawa et al. 0693 (TI). Peru, 19 Nov. 1965,  
F. Maekawa et al. 1259 (TI).

*H. heterophylla* (R. et P.) Hook.: Costarica,  
Cartago Provincia, 14 Feb. 1971, Gillis and  
Powman 10234 (KYO).

*H. latifolia* (HBK.) Roemer: Peru, 13 Dec.  
1965, F. Maekawa et al. 1921(2) (TI).

*Osteomeles* Lindl.

*O. anthylidifolia* Lindl.: Ryukyu, Isle. Ohgami,  
Y. Miyagi et al. 38360 (TUSG).